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HABITS OF *MICROTUS CALIFORNICUS* REVEALED BY AUTOMATIC PHOTOGRAPHIC RECORDERS

OLIVER P. PEARSON

Museum of Vertebrate Zoology, University of California, Berkeley, California

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INTRODUCTION

This report is based upon photographic records, made over a period of 19 months, of animals using the runways of meadow mice, *Microtus californicus* (Peale), in grass and weed habitat at Orinda, Contra Costa County, California. When an animal passed along a runway in front of one of the two recorders, it was photographed and the date, time, temperature, and relative humidity were recorded. Many of the mice had been live-trapped and marked distinctively to make them individually recognizable in the photographs. Details of the apparatus, habitat, and procedure have been described elsewhere, and the 27 other species of animals using the *Microtus* runways have been listed (Pearson 1959). Meadow mice were by far the most frequent users, with harvest mice, *Reithrodontomys megalotis* (Baird), the second most active species. No clear evidence was obtained of any interaction between these two species.

AMOUNT OF ACTIVITY IN A RUNWAY

NUMBER OF PASSAGES PER 24 HOURS PER RUNWAY

The recorders were placed at what appeared to be frequently-used *Microtus* runways and were left in place until traffic had almost ceased or until it was thought that more traffic would be recorded at some other runway. As a result of 778 recorder-days and nights in runways selected in this manner, 6077 passages of *Microtus californicus* were recorded. This gives an average of 7.8 passages of *Microtus* per 24

hours, or one passage for each 3 hours. Two frequency distributions of the number of passages per 24 hours during part of the year may be seen in Figure 1. The number of passages by *Microtus* varied irregularly from month to month, reflecting not only changes in luck in the placement of the recorders and changes in the home ranges of animals being recorded, but possibly changes in the amount of activity of individual mice in different seasons. The greatest activity was in October of 1956 when an average of 19.4 passages of *Microtus* per 24 hours was recorded. In December of 1956 only 2.0 passages per 24 hours were recorded. The busiest single day (6 a.m. to 6 a.m.) in any one runway was May 12-13, 1957, when 5 or 6 adult *Microtus* passed in front of one of the recorders a total of 67 times.

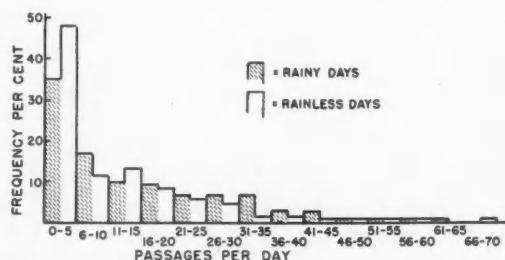


FIG. 1. Comparison of activity of *Microtus* in runways on 106 rainy recorder-days and on 120 comparable rainless recorder-days from October through May.

NUMBER OF MICE PER RUNWAY, AND
COMPOSITION OF THE TRAFFIC

The number of individual mice providing the traffic in any one runway was difficult to determine accurately because it was not possible to catch and mark all of the individuals without causing too much disturbance to the population. In many instances, however, much of the traffic was provided by marked individuals. During December, 1956, when there was little traffic in either of the runways being studied, one of the recorders was situated at a runway in which 38 of the 50 passages were by 9 marked mice. Three of these mice were fully adult and 6 were smaller; 4 were males, 4 females, and 1 sex unknown. The unmarked individuals that passed 12 times were all listed as baby or young (less than 6 weeks old) and may have belonged to a single litter. There were probably more than one of these young individuals but certainly less than 12, so the total number of mice using this runway during December was between 10 and 21, probably about 12. One of the mice did not appear until near the end of the month, at which time 5 of the other marked mice had disappeared from the runway under observation (although they were still alive and active in other runways). In view of these changes, the number of mice using this runway during any one week in December seems to have varied between 2 and 9.

An analysis of the traffic in the runway at Site 1 during the busy October season mentioned above (the relative positions of most of the recording sites may be seen in Fig. 17) yields an estimate of the number of mice using this runway as well as a fairly complete picture of the composition of the traffic. The activity in this runway will be described in detail to give the reader a glimpse into *Microtus* family life and into runway dynamics during a period when young are emerging and later when the runway is being abandoned. Five successive periods in the history of this runway will be examined (Fig. 2). The beginning of a new period was determined either by the appearance of young mice, as on October 1, or by the successful marking of additional users of the runway. The following individuals played an important role in this runway:

M13—Trapped as a pregnant adult on September 7 and marked. Recaptured September 30, at which time she was lactating. Recaptured October 8, 25, 26, November 9 and 10.

M16 and M17—Very young mice appeared in the runway on October 1 (while M13 was lactating), frequently passing the recorder within minutes or even seconds of M13. When M16 (a female) and M17 (a male) had been marked, other juveniles rarely passed, so it is assumed that M16 and M17 are offspring of M13. M16 was marked on October 11, at which time the head and body length was 91 mm. M17 was marked October 26, head and body 105 mm.

M44—Very young mice again appeared in the runway November 6, and M44, a young female with head and body 82 mm, was marked on November 10. Other young of similar size, presumably littermates, were using the runway. M14, an adult female with large nipples, may have been the mother. M13, M16, and M19 did not appear to be lactating at this time.

Big Rough—Unmarked, but probably distinctive because of unusual size and coarse pelage.

For the first part of the record (September 16-30), half of the passages were by the adult, lactating female (M13) and half of the passages were by unmarked mice (Fig. 2). Judging by the differences in body size and by texture and irregularities of the fur, there seemed to be three or more unmarked individuals.

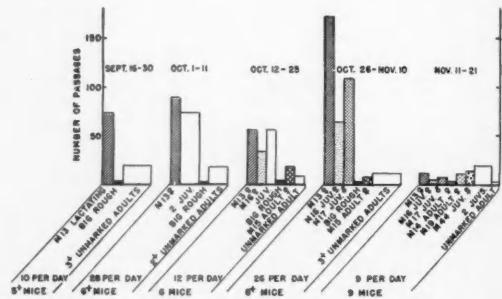


FIG. 2. Analysis of *Microtus* traffic in the runway at Site 1 during five successive time periods. Passages by unidentified mice are represented by unstippled, un-hatched columns, and are distributed evenly among the numbers of mice of appropriate age estimated to have made them.

On October 1 the first baby *Microtus* (10-25 days old) appeared in the runway, presumably the offspring of M13, and during the second period, October 1-11, the runway was heavily utilized by unmarked young. There were at least 2 young, recorded 148 times. The presumed mother (M13) passed 89 times; Big Rough passed 3 times; and 2 or more unknown adults passed 38 times. During this period, therefore, 2 or more young and 4 or more adults were using the runway.

One young mouse (presumably one of the litter that appeared on October 1) was marked and started appearing in the record October 11 (M16), and another adult (M15) appeared in this runway for the first time on October 16. Between October 12 and 25 the record was made up as follows: the mother (M13) made 56 passages; Big Rough passed 4 times; newly marked adult female M15 (nulliparous but of adult size) made 19 passages; and one or more unmarked adults made 9 passages. The young again provided most of the traffic with 92 passages. More than one-third of these were made by the marked young female (M16), which suggests that not more

than 2 young were making the remaining passages. The most reasonable census during this period, therefore, was 2 young (at least one of them a female), 2 adult females (M13 and M15), and 2 or more unmarked adults. Total: at least 6, probably not more than 8.

One other young mouse (M17), probably a littermate of M16, was marked on October 26. As a consequence, during the ensuing period (October 26–November 10) 352 of the 388 passages were made by marked individuals, providing a rather accurate analysis of the traffic. The presumed mother (M13) passed 171 times. The other adult female (M15) passed only 7 times, and Big Rough 3 times. Young female M16 made 65 passages and young male M17 109 passages. Since one of the two young made two-thirds of the passages by young during this period, it is probable that the same individual, then unmarked, was making two-thirds of the passages by young mice during the preceding period. For this reason I have assumed that there were only two young using the runway during the preceding period. The remaining 33 passages were by unmarked mice of at least three sizes. In summary: during this period the presumed mother made 44% of the passages, one of her young made 28%, and another of her young 17%. Together the three accounted for 89% of the total traffic. Another adult female accounted for 2%, and 4 or more unmarked mice accounted for the remaining 9%.

In the final period (November 11–21) more juveniles appeared and some additional adults (Fig. 2). Despite the small amount of traffic, 9 or possibly 10 *Microtus* used the runway. After November 21, harvest mice continued to use the runway, as before, but traffic by meadow mice continued to decline until many days would pass without a single passage by *Microtus*. The individuals M13, M14, M17, M19, and M44 were still alive but had shifted their activity to other runways. Further histories of some of these individuals can be followed in Figures 17 and 18.

Additional estimates of the number of mice using runways between November 1956 and June 1957 may be seen in Figures 17 and 18. Relying most heavily on those runways in which most of the passages were by marked individuals, I estimate that the total *Microtus* traffic in any one runway over a period of a few days was caused in some instances by more than a dozen *Microtus* but usually by approximately 6 individuals. The average of 52 separate estimates was 4.5 mice. This is a minimum value because two unmarked mice of similar size and appearance would have been recorded as only one.

DO BUSY RUNWAYS HAVE MORE MICE?

In the two preceding examples it was shown that in December in a runway with little traffic there were as many as 9 different mice during one weekly period, whereas in October the traffic in a busy runway was caused by 5–9 mice. To determine whether a similar lack of correlation existed between traffic

and runway population in other runways and at other times, the 52 estimates of the number of *Microtus* using a runway were compared with the average number of *Microtus* passages per 24 hours during the few days on which each census was made. A correlation graph was prepared from these data, but no correlation, either positive or negative, was discernible. Consequently, I conclude that busy runways are not necessarily used by more mice than are runways in which passages are infrequent. The data do not include, of course, runways in which there was no traffic, and they include few runways in which traffic averaged less than 3 passages per day (because the recorders were usually moved when traffic reached this low level).

The lack of correlation between numbers of mice using a runway and the number of passages can be understood by assuming that when a recorder is situated along a runway close to a nest, the individuals living in that nest make frequent passages. When a recorder is situated farther away, a few individuals from several nests make occasional passages.

DO RUNWAYS HAVE MORE TRAFFIC WHEN POPULATIONS ARE HIGH?

Ability to answer this question depends upon knowing the relative population density of *Microtus* at different seasons. Population densities were estimated from trapping results in three areas: 1) within a few yards of the recorders, 2) in a field with similar plant cover 150 meters away from the recorders, and 3) in similar habitat farther away but within 5 kilometers. Trapping close to the recorders was usually done with 10–20 Sherman live traps set for only a few hours in the evening or early morning, although occasionally for longer periods. This trapping was carried out primarily to capture and mark the animals using the runways. There were about 47 of these trapping periods close to the recorders. Trapping in the nearby field was carried out with 50 Sherman traps set 6 meters apart in a line, usually overnight. There were 9 such trapping periods. Similar trap lines were run in the more distant fields ten times.

Trapping records from the three sources agree in showing that the population density of *Microtus* was fairly low in the spring of 1956 and very high in the spring and summer of 1957. For example, 40 traps set overnight in the nearby field on April 15, 1956, caught 3 *Microtus* and 9 *Reithrodontomys*. In the light of several years of trapping in this area, I consider this to be an average catch. In contrast, 50 traps set on the same trap line at 4:30 p.m. on April 1, 1957 held at 10:30 that same evening 11 *Microtus*, 20 *Reithrodontomys*, 2 shrews (*Sorex ornatus* Merriam), and 1 house mouse (*Mus musculus* L.). The *Microtus* and shrews were released and all the traps reset at the same places. At 8 o'clock the next morning the traps held 20 *Microtus*, 12 *Reithrodontomys*, 2 shrews, and 2 house mice. The *Microtus* population was obviously high, and the catch of *Microtus*

would have been much higher if so many traps had not been occupied by *Reithrodontomys*. Similarly large catches were obtained throughout the spring and summer, and the population was still high on September 10 at the end of the recorder study. A five to ten-fold increase in trap line catches probably reflects an increase of at least 5-10 times in the *Microtus* population. A similar population increase in 1951 raised *Microtus* densities more than ten-fold on an area a few kilometers away studied by D. H. Brant.

The recorders were operating from late in January, 1956, to September, 1957. A comparison of the number of passages in occupied runways during the population high with the number of passages at a time of lower population density reveals no clear or consistent differences. Runways used regularly by *Microtus californicus* during the population low were usually being used by as many individuals as were runways during the population high. Clearly there were not 5-10 times as many mice in each runway when the population density had increased five or ten times. When the population increases, the number of occupied runway systems increases, but the traffic and the population in any one runway is not greatly increased. There is a widespread notion that populations of wild mice are controlled by the effects of an increase in contacts between the mice when the population is dense—the more contacts the greater the "stress." This may be true, but it is clear that collisions of individual *Microtus californicus* should not be thought of in terms of molecules obeying the gas laws; if each runway system tends to be occupied by a discrete population of mice, and if the population increases by a multiplication of these units, then a relatively large population increase could occur with a relatively small increase in the number of contacts experienced by any one mouse.

EFFECT OF MOON ON ACTIVITY

The number of passages by *Microtus* on the three nights of fullest moon in each month is compared below with the number of passages on the five nights of least moon each month. Three nights of fullest moon were used because it was felt that the increased data obtained thereby would more than compensate for the lower accuracy resulting from the use of traffic data on two nights during which illuminational, gravitational, and other moon effects were slightly submaximal. For the same reason five nights during the dark of the moon were used instead of just one. No allowance was made for cloudy nights, since in this area a cloudy night with full moon is, in spite of the clouds, brighter than a night with no moon.

Data are available from 19 full-moon periods of 3 days each and 17 moonless periods of 5 days each. Since two recorders were operating in separate runways during much of the study, two almost-independent samples are available for many months, giving a

total of 31 samples from full-moon periods and 28 from moonless periods. During these periods of full moon, the average number of passages of *Microtus* was 3.22 per night; on moonless nights the average number of passages per night was 4.73. These averages are crude because they include instances when recorders were moved from one runway to another in between full-moon and moonless periods. Consequently, the figures would be biased if one of the two runways had much more traffic for reasons unrelated to phase of the moon. Therefore, I have sorted out pairs of recording periods (full moons and the following moonless period) between which the recorders were not moved or disturbed. Twenty-three pairs of periods remain which give an average traffic of 3.87 passages per night of full moon and 5.00 passages per moonless night. Analysis of the difference between the average amount of traffic in each of the 23 full-moon periods and in each adjacent moonless period by the Wilcoxon signed rank test reveals that the difference in activity on moonless and moonlit nights is not statistically significant.

In the preceding analyses the comparison, or control, period for each full-moon period was a moonless period two weeks away. Because mortality and changes of home range can make a considerable difference in the amount of traffic in a runway during a 2-week period, it would be desirable to use closer control periods. Accordingly, I have compared the nightly (6 p.m.-6 a.m.) activity during full-moon and moonless periods with the daytime (6 a.m.-6 p.m.) activity during the same periods. The ratio of nighttime to daytime passages in the combined samples was almost equal (768:775), but during full-moon periods it dropped to 244:338 from a ratio of 524:437 during moonless periods. In other words, *Microtus* was more active during the daytime when the moon was full and was more active at night during that part of the month when there was no moonlight. Analysis of the differences in these proportions by the use of binomial-probability paper (Wallis & Roberts 1956) discloses a high statistical reliability for the difference.

When testing the proportions, as above, by the binomial-probability method, *each passage* contributes equally to the answer. As a result, those days and nights with much traffic have a much greater influence than those with little traffic. The rank sum test (Dixon & Massey 1957:289) gives more nearly equal influence to *each period of time*, thereby reducing the possibility that bursts of activity resulting from non-lunar causes would bias the conclusions. When the differences in numbers of passages in the daytime and at night are compared for full-moon and moonless periods by the rank-sum technique, the greater relative activity during moonless nights appears to be significant at the 5% level.

In summary, several methods of analyzing the amount of activity of *Microtus* in runways during different phases of the moon revealed a tendency for *Microtus* to be less active on full-moon nights.

EFFECT OF RAIN ON ACTIVITY

Mouse trappers frequently develop convictions that mice are more active or less active during stormy weather (e.g. Gentry & Odum 1957). *Microtus californicus* not only was active in the runways during rainstorms, but on several occasions individuals with thoroughly soaked fur were photographed. These individuals survived the soakings, as subsequent photographs showed.

In the two years during which the recorders operated, the rainy season lasted from October to May. I have tallied the number of passages by *Microtus* during the rainy 24-hour periods in these months and compared this activity with that on the non-rainy 24-hour periods within two days of the rainy days. A 24-hour period was considered to be rainy if more than a trace of precipitation was recorded at the Orinda Bowman weather station. Precipitation was measured at this station each evening at about 6 p.m. If any precipitation was recorded at this time, then the mouse activity during the preceding 24 hours (6 p.m.-6 p.m.) was listed as rainy-day activity. During 106 rainy, recorder-days the mean number of passages per 24 hours by *Microtus* was 14.9. During 120 contiguous rainless periods used for comparison the mean number of passages per 24 hours per recorder was 11.0. A comparison of the frequency distributions of the passages during rainy and rainless periods (Fig. 1) shows that the shape of the distribution is similar for both rainy and rainless periods, although there are quantitative differences. If one analyzes by the Wilcoxon signed rank test the difference between passages per 24 hours during each rainy spell and during each contiguous 2-day rainless period, the difference is found to be significant at the 10% confidence level but not at the 5% level. Accordingly it seems probable but not certain that within the rainy season *Microtus californicus* makes more passages in its above-ground runways during rainy than rainless periods.

SEX RATIO

The sex ratio of *Microtus* secured by trapping is frequently far from equality. Greenwald (1957) has shown that in *Microtus californicus* the prenatal sex

ratio is about equal but that in trapped samples females outnumber males, especially during the winter. Such a bias might result from an actual difference in the population density of males and females of trappable age, from a difference in the distance to which each sex travels, or from a difference in the frequency with which each sex comes out into the runways. The records obtained in this study make it possible to compare the frequency with which males and females appear in the runways.

Of the mice marked near the recorders and theoretically available for recording, 23 were males and 19 females. Thirty-seven per cent of the 3238 passages by marked mice of known sex were by males. However, when adjustment is made for the fact that females were available for more days and nights of recording than males, it was found that the average number of passages per 24 hours by each available male was greater than for each available female. Mice were considered to be available as long as they were known to be alive and living near one of the recorders. In Table 1 the data have been divided into winter (rainy) and summer (dry) periods; since the months of May and October are transitional, I have listed them separately. Data from the summer of 1956 have been omitted from the table because, in spite of the fact that 14 *Microtus* were marked, few of them were using the recorded runways. It may be seen in Table 1 that 14 males were available for a total of 623 days and nights and 17 females were available for a total of 1340 days and nights. The 1200 male passages divided by the 623 available male days give an average of 1.9 passages per available male per day, and the 1948 passages by females divided by the 1340 available female days give an average of only 1.5 passages per available female per day. The number of male passages (1200) departs significantly from the number expected if the ratio of passages of males to females had been 623:1340. I conclude that when all months are combined the average male tends to use the runways more frequently than the average female. Consequently, the low overall percentage of males caught in traps (Greenwald 1957) is not due to less frequent use of the runways by each male.

TABLE 1. Frequency of passage by male and female *Microtus californicus* at different times of the year. The summer (dry) period is here considered as June-Sept., the winter (rainy) period as Nov.-April. May and October, representing transition periods, are listed separately.

	MALES				FEMALES			
	No. of marked males	No. of male-days	No. of passages by males	No. of passages per male per day	No. of marked females	No. of female-days	No. of passages by females	No. of passages per female per day
May.....	5	53	176	3.3	7	110	333	3.0
June-Sept.....	8	188	252	1.3	4	208	170	0.8
October.....	1	6	28	4.7	4	102	277	2.7
Nov.-April.....	4	376	744	2.0	11	920	1168	1.3
Combined.....	14	623	1200	1.9	17	1340	1948	1.5

In Greenwald's study the proportion of males trapped rose during the summer. Table 1 shows that the number of passages per day by the average male is greater in each season than the number of passages per day by the average female, and that the frequency of both the male passages and female passages decreases by about the same amount in the summer. It appears, therefore, that the seasonal change in sex ratio of trapped samples is not due to a differential change in the frequency of use of the runways by individuals of the two sexes.

The data in Table 1 may not be so reliable as the large numbers suggest, because a recorder may sometimes have been set up near the entrance to a nest used by marked individuals mostly of one sex and as a result would have recorded disproportionately large numbers of passages by that sex. It is hoped that one sex was favored as frequently as the other. A check on this possible bias can be made by examination of the data obtained at one of the recording sites. At Site 1.2 during March and April of 1957 a single adult male (M51) and two adult females (M56 and M58) were emerging with great frequency from a burrow and passing the recorder a few inches away. Analysis of the records indicated strongly that the male and at least one of these females (M58) were a mated pair and that the photographic records provided a reliable sample of their total activity. Figures 17 and 18 show that the male was more active than the females during each of the periods into which the two months have been subdivided. The male averaged 10.6 passages per 24 hours, and female M58 averaged 4.7 passages per 24 hours. It will be shown, however, that each of the male's excursions was briefer. Whereas sexual differences in duration of excursions may affect the sex ratio of mice taken by predators, it should have little influence on the sex ratio of trapped animals. In trapped samples the frequency of excursions and the distance travelled would be more important.

DURATION OF EXCURSIONS

Microtus californicus spends much time underground in burrows that it digs itself, in tunnels abandoned by gophers (*Thomomys*), or under surface objects such as large boards. Surface runways begin at these retreats and frequently connect several of them. Nests are underground, but feeding, defecation, and urination are carried out above ground in the surface runways. On a few occasions a recorder was so situated that a record was obtained of the amount of time that mice were spending above ground during each of their excursions out into a runway. At Site 3.2, for example, the runway under observation began at a burrow opening and led to a large clump of tall green grass (*Avena fatua*) about one meter away. This grass was the only adequate food supply within several meters of the hole, no other runway approached the grass, and no other runway originated at this burrow opening. A recorder was placed at the entrance of the burrow in the hope that

all mice would be registered both on their way out and on their return, thus giving reliable records of the time spent above ground in or near this runway. The subsequent records showed (e.g. upper record in Fig. 4) that most mice were recorded going alternately to the right and to the left, thus making me confident that mice were not making numerous trips to or from the grass clump by other routes. Missed trips could lead to erroneously long measurements of the duration of excursions and of the duration of periods underground. To reduce this possibility, the few round trips lasting more than 30 minutes were excluded from the following calculations of the duration of excursions.

Between January 17 and March 11, 6 marked females and 1 marked male made a total of 188 completed round trips into the runway at Site 3.2 and back. Most of the traffic was caused by the females, and 79% of their passages were during the daytime (Fig. 12). Furthermore, they stayed above ground for longer periods during daylight hours (Fig. 3). The mean duration of emergence for 151 round trips by the 6 females between 6 a.m. and 6 p.m. was 7.4 minutes and only 2.0 minutes for 34 round trips at night. For each individual female at Site 3.2 the average time spent in the runway was much longer during the day than at night. The average duration of daytime excursions varied from 9.2 minutes for one female on 60 trips to 1.6 minutes for another female who made only 3 daytime round trips. Nighttime excursions averaged from 2.7 minutes for one female (8 trips) to 0.6 minutes for another who made only two nighttime round trips. One must conclude that the females at Site 3.2 not only avoided visiting this clump of grass at night but that when they did visit it during the night, they hurried home. Perhaps the nighttime visits were to defecate rather than to feed.

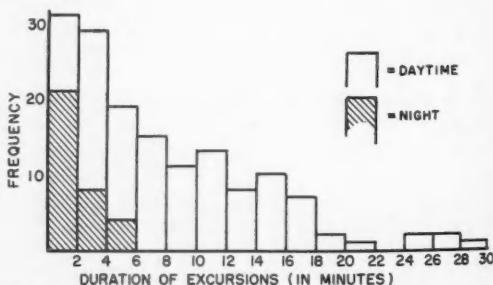


FIG. 3. The frequency of excursions of different durations made by females at Site 3.2.

The two females that used the runway most frequently and that might therefore be considered to be the "owners" showed a tendency as the days passed to remain above ground longer on each excursion. The average excursion lengthened 10 seconds per day. This increase might be due either to the gradual increase in the length and complexity of the run-

way or to the females acquiring more confidence in their surroundings each day.

The one marked male that made round trips into the runway at Site 3.2 made two trips during the day (average 3.9 minutes) and one trip at night (17 seconds). These were briefer than the average times for the females. In addition, unmarked mice made what appeared to be 23 round trips that averaged 122 seconds during the day and 46 seconds at night. Consolidation of these figures with those for the marked females at Site 3.2 reveals that the average duration of 163 above-ground excursions during the daytime was 7.0 minutes, and 1.0 minutes for 48 excursions at night. There was a distinct tendency for the individuals using the runway most frequently to remain above ground longer than did the infrequent users.

Data from a few selected other runways (Table 2) confirm most of the conclusions derived from analysis of the activity of the mice at Site 3.2. Above-ground excursions by females lasted longer than those by males, and daytime excursions by both sexes lasted much longer than excursions at night. This activity pattern was shown by adult female M58 and adult male M51 in spite of the fact that they were using the same runway. The average duration of all 413 round trips of both sexes was 5.1 minutes (Table 2).

TABLE 2. Mean duration of excursions by *Microtus californicus*.

	Date	DAILY TRIPS		NIGHTTIME TRIPS		DAY AND NIGHT COMBINED	
		N	minutes	N	minutes	N	minutes
6 females at Site 3.2.	1/24-3/6	151	7.4	34	2.0	185	6.4
1 male at Site 3.2...	2/2-2/8	2	3.9	1	0.3	3	3.9
Unmarked at Site 3.2	1/20-3/5	10	2.0	13	0.8	23	1.3
Female M58 at Site SS1	3/28-5/6	10	10.0	43	4.8	53	5.8
Male M51 at Site SS1	3/26-5/2	34	4.0	83	3.4	117	3.5
Male M305 at Site BB	5/25-6/9	17	6.1	15	2.6	32	4.4
All males combined...		53	4.7	99	3.2	152	3.7
All females combined...		161	7.6	77	3.6	238	6.3
Both sexes combined.		224	6.6	189	3.2	413	5.1

NUMBER OF ROUND TRIPS PER DAY

The two females that used the runway at Site 3.2 most frequently and consistently averaged 3.2 and 3.0 round trips each 24 hours during February, the month of most regular usage. The maximum number of round trips in 24 hours for each was 7, and each female failed to pass the recorder on only one day (not the same day).

Activity graphs similar to those in Figure 4 were drawn for many mice. The records selected for graphing were those of mice that passed the recorders most frequently over long periods of time. Comparison of these graphs with those of the two females active at Site 3.2 reveals a general similarity but some differences. The average number of round trips per day, for example, for the last three mice

in Table 2 was 5.3, which is somewhat more than for the two most active mice at Site 3.2.

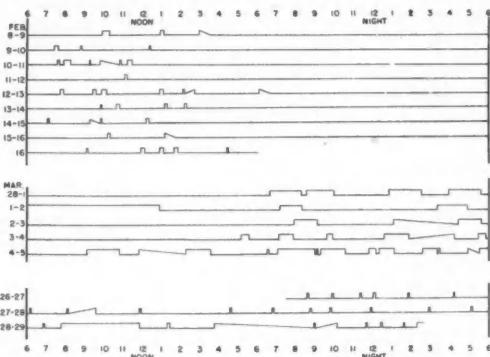


FIG. 4 (Above). Individual record of female M49 at Site 3.2 between February 8 and 16. Plateaus represent excursions; sloping lines are used when one leg of the round trip was not recorded. Note highly diurnal activity pattern.

(Middle). Individual record of male M51 at Site 1.2 between February 28 and March 5. The activity pattern is primarily nocturnal.

(Below). Individual record of Male M51 at Site SS1 between March 26 and 29.

The greatest activity shown by any one individual was by an adult, lactating female (M67) who on May 15, 1957, passed the recorder 45 times. This represents at least 22 round trips. On the preceding three days she passed 33, 14, and 10 times.

By summing the duration of excursions by a mouse out into selected runways such as the one described at Site 3.2, one obtains an estimate of the total time that it spent above ground in or near that runway. For the most habitual users of the runway at Site 3.2 during February the mean durations of excursions per 24 hours were 29.9 minutes and 15.7 minutes. When calculating these two averages, it was necessary to allow for a number of instances when the return trip was not recorded. For each of these corrections I added the mean duration of excursion for that particular female for that time of day. From the uppermost figure in Figure 4 one may judge what a small fraction of the day these females were spending above ground in this runway. Obviously this is a minimal measure of the total amount of time spent above ground when the mice are relatively exposed to hawks, owls, cats, and other predators. I think it possible that these mice spent an equal amount of time above ground in some other runway, but it seems unlikely that their total time above ground was more than three times the recorded 30 and 16 minutes per day.

The records of certain individual *Microtus* are complete enough to cover an appreciable proportion of their lifetime total of excursions. For example, one young male (M51) was marked on December 1, 1956, when he was about one month old. He was recorded only occasionally during the next 2.5 months,

but from the middle of February until early in June, when he disappeared at an age of about 32 weeks, he was recorded on 92 of the 104 days during which the recorders were operating. During his lifetime he passed the recorders 712 times, which means that he probably completed at least 356 excursions from a burrow into a runway and back to a burrow. To correct for the weeks during which he was not being recorded, one can add his average number of passages per 24 hours (which is 7.1) and arrive at a probable minimum, post-weaning number of above-ground round trips of 612. This gives a rough idea of the number of above-ground excursions that an adult *Microtus* has succeeded in making without being caught by predators or succumbing to other hazards. The average duration of 117 timed round trips made by M51 was 3.5 minutes. Six hundred twelve such excursions would add up to at least 36 hours spent out in the runways during his 32 weeks of life.

The preceding conclusions rest heavily on the assumption that the short, widely-spaced, above-ground excursions of the mice at Site 3.2 are typical of the above-ground activity of the species. Quite different and, I believe, erroneous conclusions could be reached by examining unselected records. For example, see the record of male M51 between February 28 and March 5 in Figure 4. It would not only be difficult to say whether the plateaus or the valleys represented excursions, but one would be tempted to conclude in either event that the animal was spending many hours of each day in the runway. However, as soon as the recorder was moved a few meters, the pattern of activity of the same mouse appeared to be totally different (March 27-29 in Fig. 4). I believe that the March 27-29 pattern is the simple out-and-back record and that when the earlier record was obtained the instrument may have been placed along a runway between two underground retreats that the mouse tended to use alternately.

Recordings should be made of mice living in nest boxes with only one exit so that all excursions can be recorded. Unfortunately I was not able to induce these *Microtus* to live in nest boxes.

TIME UNDERGROUND

Analysis of the length of time spent underground by mice in the runway at Site 3.2 must take into account the possibility that there were other exits from the underground retreat. With this in mind I have treated the data in the following manner. I have averaged the daytime periods when each mouse was apparently underground; I have averaged the nighttime periods apparently spent underground; and I have averaged the periods when a mouse went underground during the day and did not reappear until the next day. Any such periods longer than 24 hours were not counted.

When one of the two busiest females analyzed at Site 3.2 disappeared down the hole, a predator or a trapper could expect her to return, on the

average, in 5.04 hours. If she disappeared down the hole during the daytime and were going to reappear before 6 p.m. she would return on the average in 1.78 hours. If she disappeared during the daytime and were not going to reappear until after 6 a.m. the next day (a frequent occurrence since these females were markedly diurnal), then she would return on the average in 16.12 hours. Additional breakdown of the time underground is summarized in Table 3. It may be seen that nighttime periods underground appear to be the briefest. However, rarely did the mice go underground at night and reemerge before morning; this average therefore is influenced strongly by three periods underground that lasted less than 6 minutes.

TABLE 3. Duration of periods spent underground by two female *Microtus californicus* (combined) at Site 3.2.

	N	Average Duration
Daytime periods underground.....	91	1.78 hours
Nighttime periods underground.....	7	1.32
Underground periods lasting overnight.....	27	16.12
Other (from day into night, or night into day).....	7	8.31
Total.....	132	5.04

RHYTHM OF ACTIVITY

Caged *Microtus* show a fairly definite rhythm of activity with a period of a few hours (cf. Durup 1956). My analysis of the activity of mice, both individually and collectively, recorded at different sites and in different months, revealed no such clearly defined activity cycles. Male M51, for example, was quite active at Site SS1 between March 26 and April 24. His average underground time was 1.7 hours, but his activity periods in this runway were not evenly spaced, as may be seen in the samples of his activity shown in Figures 4 and 19. The daily activity pattern of the two most frequent users of the runway at Site 3.2 in February usually consisted of three daytime excursions lasting 7.8 minutes followed by an overnight underground period lasting 16 hours. There was not a strong tendency for the daytime excursions to be evenly spaced. Figure 5 shows how much the periods between excursions varied. The average period was 1.7 hours, but in most instances the period was only a little more than 1 hour. A second peak at slightly more than 2 hours in the distribution in Figure 5 also suggests that there is a tendency toward a basic daytime activity cycle lasting slightly more than one hour.

Believing that a rhythm of activity might be expressed at some other season, I analyzed the records of the 6 meadow mice using the runway at Site 1 during October, 1956. Figure 6 shows that these mice exhibited a tendency to concentrate their activity at certain hours of the day, especially when the time is measured from sunset. Peaks of activity occurred at

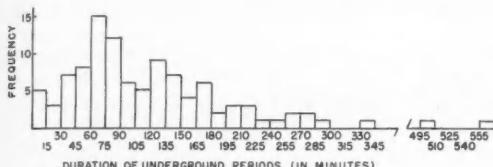


FIG. 5. The frequency of underground periods of various durations of three females at Site 3.2; includes only daytime underground periods (between 6 a.m. and 6 p.m.) in which the mouse reappeared before 6 p.m.

sunset, sunset plus 3.5 hrs, sunset plus 5.5, sunset plus 8.5, etc. The period between peaks varied so much that one cannot be certain that a true cycle is being expressed. If in this species there is a basic cycle with a period of a few hours, such as a hunger cycle, it is greatly altered by seasonal and environmental influences. When the data in Figure 6 are plotted from sunrise instead of sunset, similar but less distinct peaks are discernible.

A different pattern of activity with a 24-hour rhythm is apparent in the summer months and is described in the next section.

TIME OF DAY OF ACTIVITY IN THE RUNWAYS

ANALYSIS BY MONTHS

In an earlier report (Pearson 1959, Fig. 2) a summary of the hours of passage of meadow mice showed that when all records were combined meadow mice were active at all hours of the day and night. When the records are analyzed by months, however, distinct seasonal changes in activity pattern are revealed (Fig. 7). During the autumn, winter, and spring months, there were many passages at all hours, but during the summer few passages were recorded during the middle of the day. In fact, in each of the months of June, July, and August nearly half of the passages were recorded in the three hours following sunrise. During these summer months, minor peaks of activity occurred near sunset and in the middle of the night (Fig. 7). These three peaks (sunrise, sunset, and midnight) were clearly shown in the summers of 1956 and 1957 and at both recorders, so there can be little doubt that they reflect a real pattern of activity.

In general it appears that activity is more uniform throughout each 24-hour period in the wet months and is concentrated in the morning during

the dry months. In neither 1956 nor 1957 was there any precipitation between May 21 and September 15. The March, April, and May graphs in Figure 7 are based almost entirely on 1957 records. During this spring there were 14 rainy days (4.03 inches of precipitation) in March, 5 rainy days (2.41 inches) in April, and an unusual 13 rainy days (6.08 inches) in May. The graphs show a trend through March and April toward the summer activity pattern, but the trend is reversed in May, probably as a result of the increased rainfall. If the data for May are divided into a rainy three weeks (May 1-21) and a dry week (May 25-31), the appearance of the activity pattern for the dry week approaches that of the summer months, and the pattern for the rainy three weeks is similar to the winter pattern.

Individual mice that survive from spring into summer, or from summer into autumn, change the hours of their activity to suit the season, young mice adopting the appropriate seasonal pattern.

ANALYSIS BY SEX

Males and females at one of the recorders (Site 1.2) in February and March were active at the same times of day (Fig. 13). The data from two other recording sites provide further information for comparing activity patterns of males and females. A single adult male and female provided most of the traffic at one recorder during April, 1957, and may have been a mated pair. The 170 passages by the female were distributed throughout the 24 hours in the same fashion as the 362 passages by the male. At another site from October 26 to November 14, 1956, the distribution throughout 24 hours of the 266 passages by females was almost identical with that of the 114 passages by males.

ANALYSIS BY AGE

The hourly distribution of passages by young and adults was compared using the data from one of the recorders in April and from the other in May. These were two series of records containing frequent passages by both adults and young. From the size of the mice and the appearance of their pelage in the photographs, they were classified as baby, juvenile, small adult, or adult. In none of the three younger age classes did the activity pattern differ appreciably from that of the adults.

ANALYSIS BY LIGHT

The fact that *Microtus* is active at all hours during the autumn, winter, and spring suggests that light

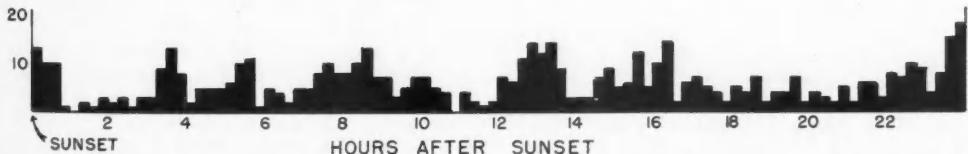


FIG. 6. Frequency of passages at different 15-minute intervals following sunset. Based on all *Microtus* passages at Site 1 during October.

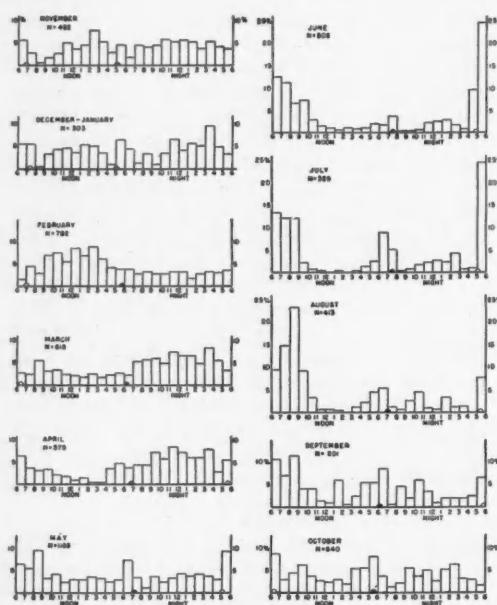


FIG. 7. Frequency distribution of the time of *Microtus* passages in different months. Open semicircles along the base lines indicate mid-month times of sunrise; solid semicircles represent sunset.

intensity does not play a dominant role in regulating the activity pattern. This suggestion is further supported by the fact that under especially favorable feeding conditions, mentioned later, meadow mice readily come out into bright sunshine in the afternoons in the middle of summer.

Since light does not seem to be one of the environmental factors that imposes the highly restricted diel cycle in the summer months, two other possibilities should be investigated—temperature and water.

ANALYSIS BY TEMPERATURE

June, 1957, was selected for analysis of temperature conditions because this was the summer month for which the most *Microtus* passages were available. Figure 8 was constructed by averaging the temperatures in the instrument shelters at each half-hour during which the recorders operated in June. The two curves, therefore, represent the temperatures in the two runways on the hypothetical average June day during which the recorders operated in 1957. On no day was a temperature recorded for every half-hour, so it was necessary to construct a graph of the temperatures for each day and to interpolate between points when they were widely spaced. This interpolation was accomplished by using as a model the appropriate part of a curve based on abundant points and recorded at that same runway on a day on which the maximum and minimum values, as recorded at the Orinda Bowman weather station three kilometers away, were similar to those on the day in question.

The differences in the two curves in Figure 8 result largely from the placement of the two instrument shelters. Although they were only 14 meters apart, one shelter (SSI) received the sun earlier in the morning and was shaded for much of the afternoon.

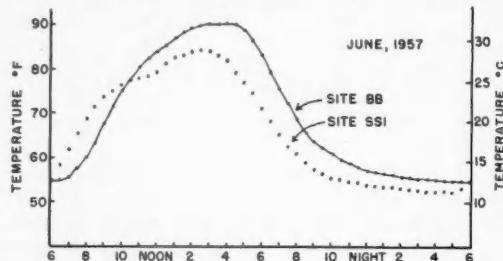


FIG. 8. Temperatures at the two recorders during the average June day, 1957.

Comparison of Figure 8 with the June activity graph in Figure 7 gives the impression that *Microtus* is either avoiding the hot parts of the day or showing a preference for activity during the coolest time. Such a conclusion should not be drawn, however, without calculating how much time was available to the mice at each temperature. It would not be wise to conclude, for example, that since only two of the 458 *Microtus* passages in June of 1957 occurred when the temperature was over 35°C the mice were avoiding high temperatures. Perhaps there were only a few hours during the month when the temperature was over 35°C. The solid line in Figure 9 shows how much time was available at the different temperatures. It was prepared by making a frequency distribution of the half-hourly temperatures on each of the daily temperature charts at each of the two recorders operating in June of 1957. There were, for example, 103 half-hour periods with a temperature of 15°C (4.5% of all half-hour periods) but only 11 periods (0.5%) at 35°C. Compared with this frequency distribution of available temperatures in Figure 9 is a frequency distribution of *Microtus* passages at different temperatures at these same two recorders in June of 1957. If *Microtus* showed no preference for above-ground activity at certain temperatures, and if the sample were very large, the peaks and valleys of the two curves would be in perfect register. If, for example, the temperature was at 11°C for 4% of the month, then one would expect 4% of the *Microtus* passages to have occurred at that temperature. On the other hand, if *Microtus* preferred or avoided certain temperatures, the mouse-activity curve in Figure 9 should rise above or drop below, respectively, the available-temperature curve. The most marked discordance between the two curves is the apparent preference of mice to be active at about 15°C. Much of this preference was due, however, to an unusual burst of grass-carrying and other activity by a single mouse at one recorder early one morning when there were 35 passages within one

hour, all at 15°C, and to another burst of grass-carrying and other activity by one or more mice at the other recorder during which 36 passages were recorded within 2.5 hours, all early one morning at 15° and 16°C. Although these passages should not be ignored, it might be argued that two microtine emergencies caused 18% of the monthly traffic to pass within a few hours during which the temperature happened to be 15° or 16°, thereby giving undue emphasis to those temperatures. If we assume that all of the passages of these individuals during these two flurries were non-recurrent emergency trips and omit them from the calculations, then the peak at 15°C becomes truncated as shown by the broken line in Figure 9. The agreement between the mouse-activity and available-temperature curves then becomes closer. Judging from either the adjusted or unadjusted curve, it is clear that *Microtus* was not obviously avoiding any specific temperature or temperature range. Also, since temperatures were almost constant from midnight until 6 a.m., the early-morning increase in activity cannot be attributed solely to a preference for cool temperatures.

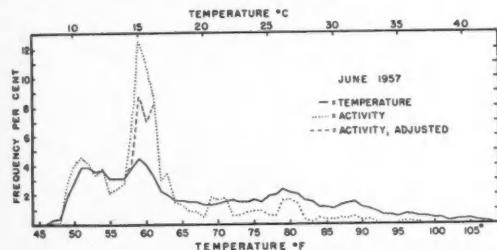


FIG. 9. Comparison of the amount of time available (in per cent) for mouse passages at different temperatures during June, 1957, with the per cent of *Microtus* passages (activity) recorded at those temperatures. Since there was a tendency to read certain temperatures on the thermometer preferentially, the curves were constructed by 3-point averaging to reduce the effects of this bias.

ANALYSIS BY WATER BALANCE

Loss of water

Dice (1922) and Lindeborg (1952) have shown that in other species of *Microtus* the rate of water loss is relatively rapid and the water requirements relatively great. Presumably *Microtus californicus* is also poorly adapted for living in an arid environment, so it is interesting to learn whether its summertime activity pattern may have evolved in response to a need to reduce loss of body water or to increase intake of water.

A major fraction of the water loss of deer mice (Chew 1955) and presumably of meadow mice is by evaporation from the lungs, a warm moist surface. That fraction of evaporation that occurs from external surfaces such as the ears, eyes, and skin may also be considered to be from warm moist surfaces.

It can be shown that the rate at which water is lost from a warm surface depends, if other things are equal, upon the pressure of water vapor in the surrounding air. When the surrounding vapor pressure is high, evaporation will be slow, and vice versa. For discussion of this see Salt (1952) and Thornthwaite (1940). The relative humidity of the surrounding air is of little importance because evaporation can take place from a warm surface into cooler air even if the air is saturated (100% relative humidity). Accordingly, from the temperature and relative humidity data recorded by the apparatus, I have calculated the vapor pressures encountered by meadow mice in their runways during June of 1957. The vapor pressure curves for the two recorders are shown in Figure 10 and were prepared in the same fashion as the temperature curves. Note how different the vapor pressures were at the two locations only 14 meters apart. Site SS1 (the upper curve) was much more humid during the day, due presumably to the fact that in its partly shaded location temperatures rose fairly high during the day but relative humidities did not drop nearly as much as at the more exposed Site BB. Despite the profound difference in vapor pressures at the two sites, the activity pattern of the mice was not markedly different. In fact, the greatest difference in activity pattern at the two stations was a tendency for the mice at Site BB to remain active later in the morning, and at this station the vapor pressure was *lower* at this time of day, thereby exposing the mice to more rapid evaporation.

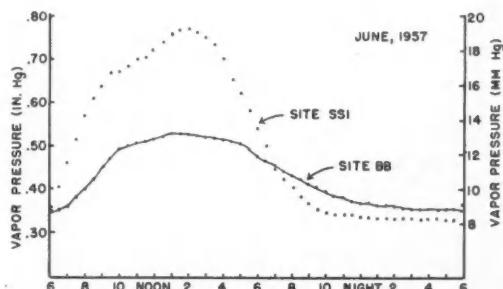


FIG. 10. Vapor pressures at the two recorders during the average June day, 1957.

Figure 11 shows the amount of time available to the mice at the different vapor pressures. It was prepared in the same fashion as the available-temperature curve in Figure 9. The curve for frequency of mouse activity at different vapor pressures matches it closely, except for the peak near 10 mm of mercury due to the early-morning bursts of activity mentioned above. In view of the close concordance of these two curves, I conclude that the mice were making no effective effort to avoid any particular range of vapor pressures, and that their early-morning activity is not controlled by vapor pressure. Furthermore, the vapor pressure that exists at the time of greatest

activity is about the same as that existing throughout a large part of the night.

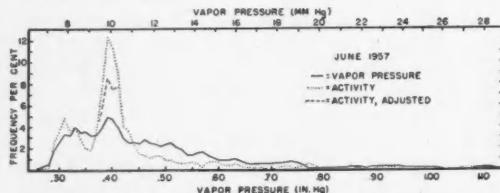


FIG. 11. Comparison of the amount of time available (in per cent) for mouse passages (activity) at different vapor pressures during June, 1957, with the per cent of *Microtus* passages recorded at those vapor pressures. Three-point averages used as in figure 9.

It is important to note that activity was greatest when vapor pressure was lowest. In other words, the mice were most active in the runways at the time when they would lose water most rapidly. Unless forced to pant, salivate, or perspire to keep cool, these mice would have conserved water most effectively by limiting their above-ground activity to the middle of the afternoon.

Intake of water

There was as usual no precipitation in June. Consequently, water intake must have come from succulent vegetation, from the combustion of food-stuffs, or from dew. *Microtus californicus* is unable to survive on the metabolic water derived from the combustion of seeds and other dry foods (unpublished data). Green vegetation was becoming scarce in June and, later in the summer, was lacking in some habitats occupied by *Microtus*, so it is concluded that *Microtus* had other sources of water. Succulent underground stems and roots may have been one of these sources, and dew may have been another. Chew & Hinegardner (1957) have shown that white mice can survive on only 10% of the desired amount of water. Dew, therefore, could provide an important part of the water requirements of mice in the wild. In the summer at Orinda very little dew collects before midnight, and on the usual clear, calm nights, the amount of dew available to mice is maximum early in the morning. A mouse coming out at this time, despite the maximum rate of water loss from its lungs, has available the maximum amount of water. I believe, therefore, that the summer activity pattern is controlled primarily by the need for water and its availability as dew early in the morning. The lesser peaks of activity in the late afternoon and in the middle of the night may reflect an innate hunger cycle or evacuation cycle.

There remains to be answered the question why the mice avoid using the runways in the afternoon during the summer. It is possible that activity in the hot sunshine would cause the mice to evaporate an excessive amount of water to keep cool. It is probable, also, that during the day vapor pressures

are higher in the burrows than in the runways (Schmidt-Nielsen & Schmidt-Nielsen 1950) so that the scant water supply would be conserved by remaining underground.

The supposition that water-intake from dew is an important regulator of mouse activity in summer is supported by the fact that as soon as mice are released from water shortage in the autumn, they abandon the early-morning preference and are active at all hours of the day and night. This release may be brought about by autumn rains or by the fact that on many autumn days, when the sun is low in the sky and the temperature cool, dew remains on low vegetation all day long.

Under certain conditions *Microtus* is spared much of the danger of dehydration, even in the middle of the summer. For example, one kilometer from the study plot a dry, grassy-weedy slope similar to the study plot met abruptly a large grassy lawn that was kept green by frequent mowing and watering. Meadow mice were abundant here in the summer of 1957, as they were near the study plot, and frequently left the shelter of the dry tall grass and weeds to feed on the lawn, where they were seen on many occasions even in the middle of the afternoon. For example, at 4 p.m. on July 13, a hot, sunny afternoon, while walking quietly along 45 meters of the boundary between the dry slope and the lawn, I saw 12 *Microtus*. Since mice rarely passed the recorders during the middle of the afternoon at this season (Fig. 7), and since they rarely could be seen at this hour in the numerous runways only a short distance away from the lawn or in the runways near the recorders, I conclude that the mice living near the edge of this lawn were able to alter their activity pattern because a supply of water (contained in green grass) was available to them at all hours.

A LOCAL DIFFERENCE IN ACTIVITY PATTERN

When the maintenance of proper water balance is easy, as during the rainy season, it might be expected that other less important factors could influence the activity patterns of individual mice or of local populations of mice. Such seems to have been true for two populations whose activity patterns were recorded between February 16 and March 20, 1957. The two recorders were 9.5 meters apart (Sites 3.2 and 1.2) and, since the mice passing one of the recorders rarely appeared at the other recorder, the populations may be considered to be almost distinct. Figure 12 shows that activity at Site 3.2 was primarily (71%) during the daytime and at Site 1.2 during the night (74%). In search of reasons for this difference I noticed that almost all of the traffic at Site 3.2 was provided by 6 adult or young-adult females, and much of the traffic at Site 1.2 was provided by 2 males. However, if one graphs the activity of only the females at Site 3.2 and compares this graph with graphs of the activity of females at Site 1.2 and of males at Site 1.2 (Fig. 13), it becomes obvious that the females at Site 3.2 were di-

urnal but the females using the runway at Site 1.2 conformed to the nocturnal pattern of the males in that runway. Consequently the difference in the activity patterns at the two locations was not due to a difference in behavior between males and females in the two runways.

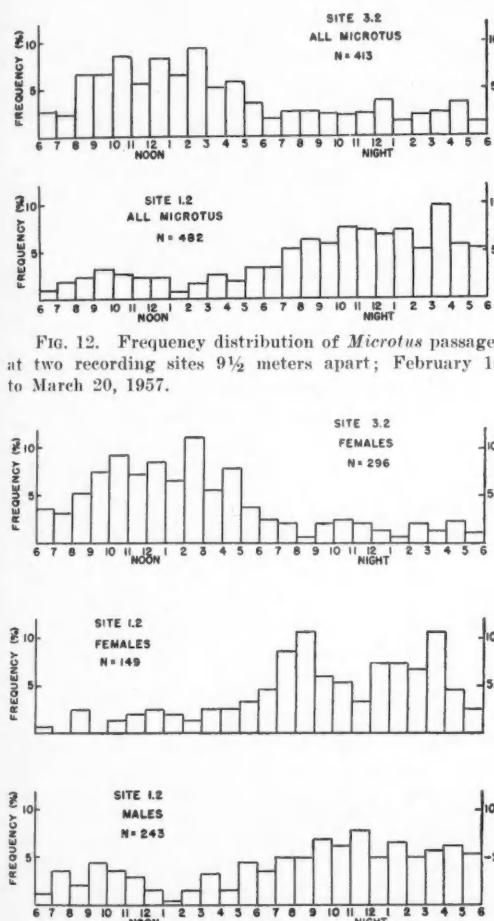


FIG. 12. Frequency distribution of *Microtus* passages at two recording sites 9½ meters apart; February 16 to March 20, 1957.

FIG. 13. Comparison of the frequency distribution of the passages of females at Site 3.2 with that of females at Site 1.2 and males at Site 1.2; February 16 to March 20, 1957.

Although the two sites were only 9.5 meters apart and of similar slope, exposure, and vegetation, it was felt that there might have been microclimatic differences great enough to explain the different activity patterns, and accordingly climatic curves for the two recorders from February 16 to March 20 were constructed in the same manner as described above for June. Figure 14 shows that the average daily temperature and vapor pressure curves for the two sites were quite similar, probably too much alike to account for the behavioral difference. At Site 1.2,

the curve representing frequency of mouse passages at different temperatures conforms rather closely to the curve representing availability of different temperatures (Fig. 15), and there is a similar close concordance of mouse activity with availability of different vapor pressures (Fig. 15). Such concordance shows that the mice at Site 1.2 were neither seeking nor avoiding a specific range of temperature or vapor pressures. However, at Site 3.2 the mice failed to use the runway during most of the cold, dry hours available to them. This lack of agreement between the mouse activity curve and the available-temperature and available-vapor-pressure curve is shown clearly in Figure 16. I am unable to explain why the mice at Site 3.2 expressed this behavioral preference while those at Site 1.2 did not. It seems probable that in winter relatively small factors are able to cause a shift in the activity pattern of an individual mouse, or group of mice, whereas in summer the time of availability of water keeps mouse activity in a more rigid pattern.

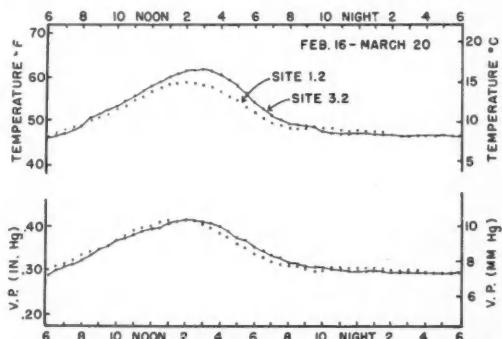


FIG. 14. Temperatures (above) and vapor pressures (below) at the two recorders during the average day between February 16, and March 20, 1957.

LONGEVITY

Mark-and-recapture studies on numerous species of *Microtus* have shown that a few individuals live more than one year, but little is known of the average life span because many if not most young die before they are first trapped (Hoffman 1958). Although the photographic recorders have few advantages over live traps for investigating the longevity of mice, so little information is available on the longevity of *Microtus californicus* in the wild that it is worth reporting the data obtained in this study. Captured mice were marked for easy identification in the photographs by clipping patches of fur. In addition, numbered metal tags were clipped onto the ears.

Forty-two *Microtus* were marked. Eleven of these were never seen again, and 8 were marked during the last three months of the study, so are of little value for longevity studies. The longest recorded life span among 9 mice marked in May and June of 1956 was 14 weeks; none of these mice was seen again after

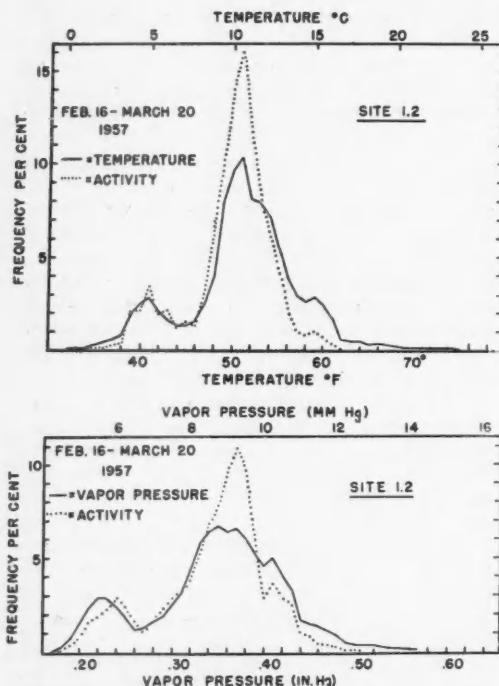


FIG. 15. Comparison of the amount of time available (in per cent) for mouse passages at different temperatures (above) and vapor pressures (below) at Site 1.2 between February 16 and March 20, 1957, with the per cent of *Microtus* passages recorded at those temperatures and vapor pressures. Three-point averaging used as in figure 9.

September 30 in spite of almost a full year of additional recording and trapping during which they might have reappeared. Seven of the 9, however, were still alive 10 weeks after they had been marked.

Seventeen mice were marked between September 6, 1956, and January 3, 1957, and had an average recorded life of 14 weeks. This average includes 3 animals that were never seen again after marking and one that was still alive at the end of the study in September, 1957. No less than 10 of these 17 marked mice survived at least 12 weeks after they were marked. Many of the mice were young when marked, so that their date of birth could be estimated. When this was done the age at last appearance of each of the 10 marked as juveniles between September 1956 and January 1957 varied from 5 to 42 weeks with a mean of 23 weeks. If each of the adults is assumed to have been more than 60 days old when marked, then the mean age at disappearance of all 17 mice during this period was more than 21 weeks.

The longevities listed in the preceding paragraphs, measured during a period when the population was building up to a peak, are comparatively long for mierotines in the wild (Bodenheimer 1949). The average longevity was probably increased by a fence,

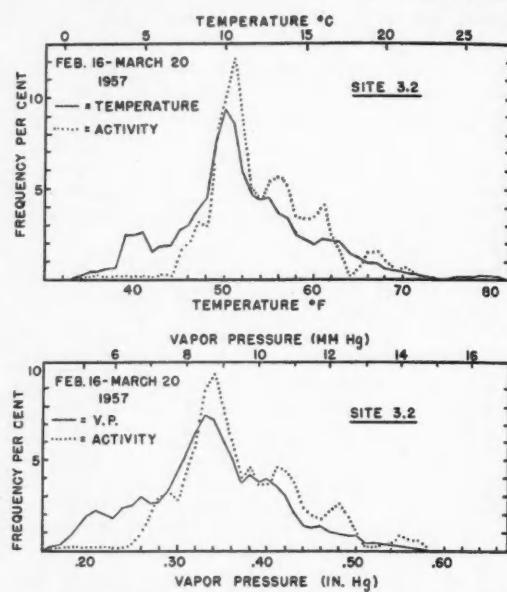


FIG. 16. Comparison of the amount of time available (in per cent) for mouse passages at different temperatures (above) and vapor pressures (below) at Site 3.2 between February 16 and March 20, 1957, with the per cent of *Microtus* passages recorded at those temperatures and vapor pressures.

0.8 meters high and made of 5 cm-mesh woven wire, that surrounded the study area most of the time. This fence reduced predation by cats and other terrestrial carnivores of similar size.

HOME RANGE

Studies by D. H. Brant have shown that 15-meter spacing of traps revealed only the longer movements of *Microtus californicus*. Simultaneous operation of two recorders at various distances apart has provided information on how far *Microtus* travels, how frequently it travels, and how long *Microtus* takes to make excursions of various lengths.

For four months the recorders operated at two stations 70 meters apart. Despite the fact that the intervening terrain was excellent *Microtus* habitat, no *Microtus* marked at one of these two stations appeared at the other. Results from operating the recorders closer together are partly documented in Figures 17 and 18 and are summarized in Table 4. For example, during the eleven measuring periods listed in Table 4 through which the recorders were 14 to 20 meters apart, only 2 marked individuals appeared at both recorders in any one measuring period. One of these individuals (M305) was marked on May 24 and appeared at Site BB one or more times on the 24th, 25th, 26th, and 28th. On the 29th it passed Site BB at 5:00 a.m., passed the other recording station 14 meters away at both 5:53 and 5:57 a.m., and was back at Site BB at 6:22 a.m. It was

then seen daily at Site BB until June 9, when it disappeared. A breeding female (M67) made a similar 14-meter one-day excursion on June 29. These are clearly examples of excursions rather than changes of home range, and were the longest ones documented. At least two other mice (M50 and M51) covered as great a distance, but their movements were associated with more lasting changes of home range and were not excursions.

TABLE 4. Amount of interchange of *Microtus californicus* between recording sites at different distances apart. Entries are listed in a sequence of decreasing distances.

Date	Distance between recorders (in meters)	Number of marked mice	Number of passages by marked mice	Number of marked mice interchanging	Number of passages by interchanging mice
August 11-21.....	20	4	38	0	0
August 22-31.....	15	6	39	0	0
September 1-10.....	15	5	38	0	0
April 24-May 1.....	14	4	61	0	0
May 2-10.....	14	5	87	0	0
May 11-20.....	14	5	254	0	0
May 21-31.....	14	3	95	1	2
June 1-19.....	14	3	75	0	0
June 22-30.....	14	4	65	1	1
July 1-9.....	14	3	101	0	0
July 10-August 7.....	14	3	68	0	0
February 16-28.....	9.5	9	372	2	23
March 1-13.....	9.5	7	295	3	9
March 14-20.....	9.5	4	45	0	0
March 26-April 8.....	5	2	243	0	0
April 9-24.....	5	2	255	1	6
March 20-26.....	2	4	18	1	1

While the recorders were 9.5 meters apart, 3 marked mice (two females and a male) appeared at both of the sites during the same measuring period. The actual amount of interchange was low, however, because only 32 of the 712 passages by marked mice were interchanges. These 32 amount to 10% of the passages made by these 3 mice and were clearly excursions within a home range, not shifts of home range. Among 13 occasions when a mouse appeared at both recorders 9.5 meters apart on the same day, the shortest elapsed time between the two records was 14 minutes. Even at shorter distances of 5 and 2 meters there was surprisingly little interchange (Table 4), and the shortest elapsed time for the 5-meter interchange was 16 minutes.

If one runway system should interdigitate with another without connecting with it, it would be possible with the two recorders to obtain frequent records of different mice occurring less than a meter apart without interchange. This situation did occur. However, few interchanges were obtained even when two recorders were operating at the extremities of a single, complex system of runways, so it is obvious that home ranges are small. Individuals probably rarely move more than 15 meters from home, and most of their activity is probably within a radius of 5 meters. It is also clear that although a *Microtus*

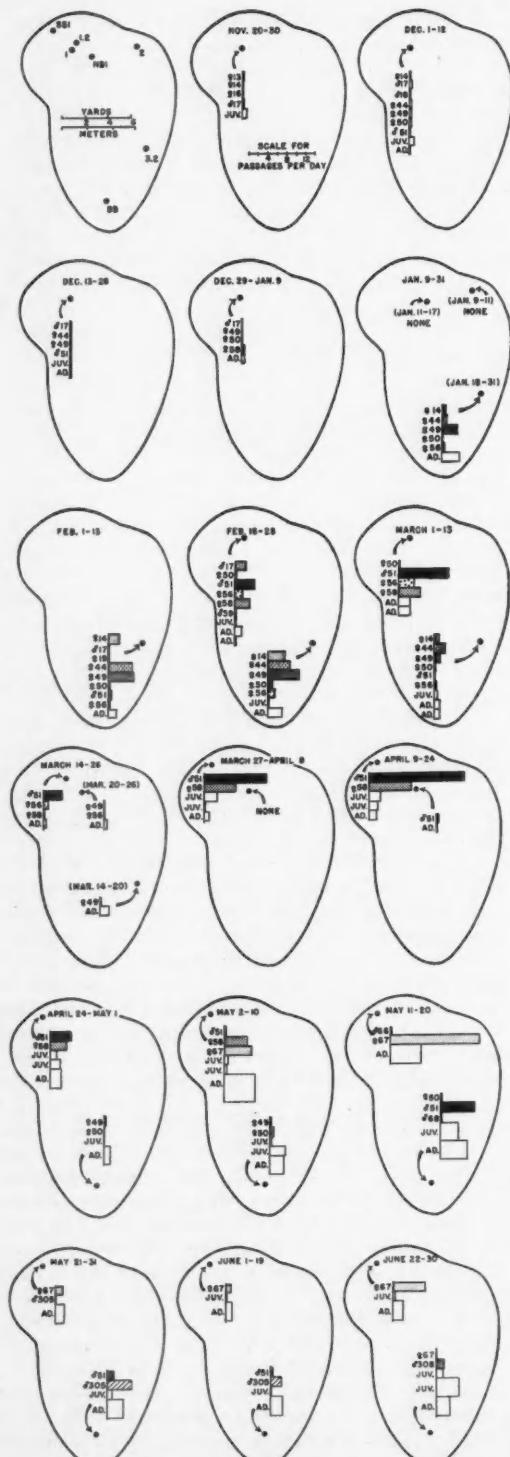
californicus is able to travel 5 or even 10 meters in a few seconds, it rarely does so.

Many of the mice followed in this study lived for months near the site at which they were marked and rarely or never appeared at other recording stations. Some, however, changed their home ranges. The history of 4 of these individuals can be followed in Figures 17 and 18. These were an adult female (M14), 2 young females (M44, M49), and a young male (M51). Two of these young were probably littermates (M49, M51), and the third (M44) may also have been their littermate. All 4 of these individuals were using the runway at Site 1 in late November or early December and all 4 abandoned this part of their range before the end of December. The reason for their departure is not known; no new mice had taken possession of the runway. The 3 females of this group were found to be 9.5 meters away when a recorder was set up at Site 3.2 on January 18. One of these 3 females (M44) disappeared abruptly on March 5. Another (M14) gave birth to a litter about March 6 and did not visit Site 3.2 again after March 11. She was found 4 meters away at Site BB on March 20 in a nest with litters of two ages. The third female (M49) gradually abandoned Site 3.2 also. She was last seen there on March 16, at which time she was probably pregnant. She was active at Site BB when the recorder was placed there on April 24 and remained active there until she disappeared on May 9. In summary, these 3 mice all abandoned Site 1 at about the same time, all abandoned Site 3.2 at about the same time, and the 2 known survivors used Site BB. During their lifetimes the greatest diameter of their travels was at least 12 meters.

The fourth mouse mentioned above was M51, whose history is illustrated in Figures 17 and 18. He too abandoned Site 1 at about the same time as the other three, and he too appeared at Site 3.2, but not until more than a week after the others. He visited there only until February 11, when he returned 10 meters to the vicinity of Site 1 for a long and busy career. On May 2 he disappeared again and 10 days later appeared 14 meters away at Site BB. He remained at Site BB until he disappeared on June 6.

BIOGRAPHY OF M51

One of the most valuable results of the use of photographic recorders such as the ones used in this study is the accumulation over a period of time of a great number of glimpses into the affairs of individual mice. With kill-trapping one must piece together the biography of a hypothetical mouse by a synthesis of the terminal instants of many mice. With live-trapping and nest box techniques one can follow the lives of individuals but only with considerable disturbance to those individuals. With photographic recorders disturbance is minimal. Many fascinating snatches of the lives of several *Microtus* can be pieced together from the film strips (supplemented by the data from the small amount of trapping necessary to



mark the mice), but I have found no brief way of summarizing these snatches or of presenting them at reasonable length. I have chosen instead to show by a series of graphs a rather detailed accounting of the life of a single individual, M51, and some of his associates. The following comments refer to each of the graphs in Figures 17 and 18.

November 20-30—Young of about 2 weeks of age started appearing at Site 1 on November 6. The young appeared to be a litter later marked as M49, M50, and M51, and possibly M44 and M52. M51 was probably represented among the young recorded in this November 20-30 period. Also using this runway were two older juveniles (M16 and M17), their mother (M13), and an additional parous adult female (M14). *Microtus* traffic in this runway was declining at this time, although there was much traffic by *Reithrodontomys*.

December 1-12 and 13-28—M51 was marked on December 1. There was little traffic by *Microtus* during these two periods, much of it provided by M51 and his sibs.

December 29-January 9—Very little traffic. M51 has moved elsewhere. A young female (M58) a few weeks younger than M51, was marked on December 29 and later, with M51, will dominate this runway. Seven or more *Reithrodontomys* were still using this runway.

January 9-31—Moved the recorder to Site 2 (January 9-11) and to Site NB1 (January 11-17), but recorded only *Reithrodontomys*. Then moved to Site 3.2 where four of the mice from Site 1 were found to be active. M51 still missing. M56, who first appeared January 22, was an immature female.

February 1-15—M51 used the runway occasionally along with his sibs; much of the traffic was by mice formerly active at Site 1.

February 16-28—A second recorder was now operating, at Site 1.2. This was less than a meter from the original Site 1, 9.5 meters from the other recorder at Site 3.2. M51 has left Site 3.2 and returned to near where he was originally recorded when young.

Figs. 17 and 18. A history of male *Microtus* M51 and his associates during 17 consecutive time periods from November 20, 1956, to June 30, 1957. The irregular oval shapes represent the fenced portion of the study area. The black dots in the first diagram at the upper left corner of the page show the locations of the recording sites mentioned in the text. In the succeeding entries the *Microtus* traffic at each of the recorders is illustrated by bar graphs that show the average number of passages per day for each individual during the given time period. A scale for passages per day, applicable to all of the diagrams, is given in the second diagram. Male M51 is represented in each diagram by a solid black bar; other marked individuals are represented by patterned bars, and unmarked individuals, the number of passages per day is distributed equally among the estimated number of unmarked individuals of the same size giving those passages.

At least one of his littermates (M50) made a few passages in his runway, and a possible male sib (M17) was fairly active in the same runway until February 26, but disappeared on February 28. More than half of the traffic at Site 1.2 was by M51 and M58, and over 86% of the traffic was by 6 marked individuals (3 males and 3 females) all of which were 3 to 5 months old; the females were nulliparous. M58 became pregnant about February 26; M51 was by far the most active male in this runway at the time and perhaps the sire.

March 1-13—M51 and two females were quite active at Site 1.2, also one or more unmarked adults. On one day M51 visited Site 3.2; 2 or 3 of his female sibs were active there. Two of the females also cross-visited. Brother-sister copulations were easily possible at this time as well as on several other occasions.

March 14-26—Most of the traffic at Site 1.2 was by M51 and two breeding females. Pregnant female M56, however, moved away on March 21 and never returned to this site although she was trapped nearby in lactation on May 9. M58 gave birth about March 19. Because of little traffic at Site 3.2, the recorder there was moved on March 20 to NB1. M51's sib M49 appeared at both of these sites.

March 27-April 8—Moved recorder from Site 1.2 to a busier-appearing runway 2.5 meters away (SS1); much traffic by M51 and M58, who was now pregnant again. Very small young less than 3 weeks old started appearing in the runway on April 2. Since M58 was the only female using the runway regularly, appeared to be pregnant when trapped on March 13, and was recorded as lactating-pregnant when trapped on April 9, she was presumed to be the mother of these new young. No traffic at NB1 except by *Reithrodontomys*.

April 9-24—Site SS1 dominated by M51 and M58; young of two sizes using the runway also. M58 probably gave birth about April 14. M51 visited Site NB1 5 meters away on two days.

April 24-May 1—M51 and M58 and young of two sizes still active at Site SS1; young of about 2 weeks of age, probably offspring of M51 and M58, appeared April 30. Two or possibly 3 unmarked adults have now begun to use the runway also. The other recorder has been moved from NB1 to Site BB, and here M51's two sisters (M49 and M50) were active. Both were parous at this time.

May 2-10—Two or 3 unmarked adults appeared with increasing frequency at SS1 and in addition M67 (an adult parous female with distinct pelage) appeared for the first time on May 7. M51, who has appeared at Site SS1 almost daily through May 2, disappeared until May 8, when he passed once, and once on May 9; then he left this site permanently, perhaps driven out by one of the new adults now using the runway. On May 5 a garter snake (*Thamnophis*) carrying a juvenile *Microtus* in its mouth passed the recorder at SS1. Passages by juveniles, which had been frequent up to this time, stopped

immediately and were not resumed until June. M51's longtime consort M58 appeared daily through May 7, then she too left, but was still active 3 meters away in September. Her departure may have been due to the destruction of her litter by the snake or to the occupation of the runway by other mice. At the end of this period the runway was used mainly by the new adult female (M67) and two or more unmarked adults. M51's two sisters (M49 and M50) were still active at Site BB.

May 11-20—Site SS1 was frequented by M67 (lactating) and two or more other adults. M51 appeared at Site BB on May 12; his last surviving sib (M50) had been recorded for the last time 10 hours earlier.

May 21-31—Site SS1 was still used primarily by M67 and one or more unmarked adults. M51 was still active at Site BB along with a small-adult male and three or more unmarked mice.

June 1-19—Site SS1 was still dominated by M67 and one or more unmarked adults. Two or more adults were active at Site BB. In addition M51 was recorded at Site BB on June 1, 2, 3, 4, and 6, but then disappeared.

June 22-30—M51 not seen again, although a recorder remained at Site BB and another near his former range (Site SS1) until September 10. The predominant female at SS1 (M67) raised a litter and remained there until mid-August. In early September she was sharing a runway 3 meters away with M58, who was M51's former mate and who, like M51, left Site SS1 when M67 and her associates moved in.

FAMILY ASSOCIATIONS

Traffic at Site SS1 during late March and April was especially well documented and revealed an enduring family association. During these weeks male M51, female M58, and their offspring appeared regularly at the recorder (as many as 59 passages per day by the members of the family), and there was little traffic by other mice (Fig. 18). The passages of the male seemed to be unrelated to those of the female. Although they sometimes passed along the runway within a few seconds of each other, neither followed the other one regularly. Both the male and the female tended to avoid activity in the middle of the day. The female became more active at the time of the appearance of her litter in the runway and just before the birth of her next litter. At both times the female made several passages while carrying grass and leaves toward the nest. The male (M51) became most active in the runway when the female was late pregnant, and this was also the only time when a known adult male was seen carrying cut pieces of vegetation. There was no evidence that the female drove the male out of the runway when she was pregnant or lactating. The male on numerous occasions passed the camera within four minutes of young mice, and, since young mice continued to use the runway, he apparently did not harm them or drive them away. Figure 19 shows in detail the time of

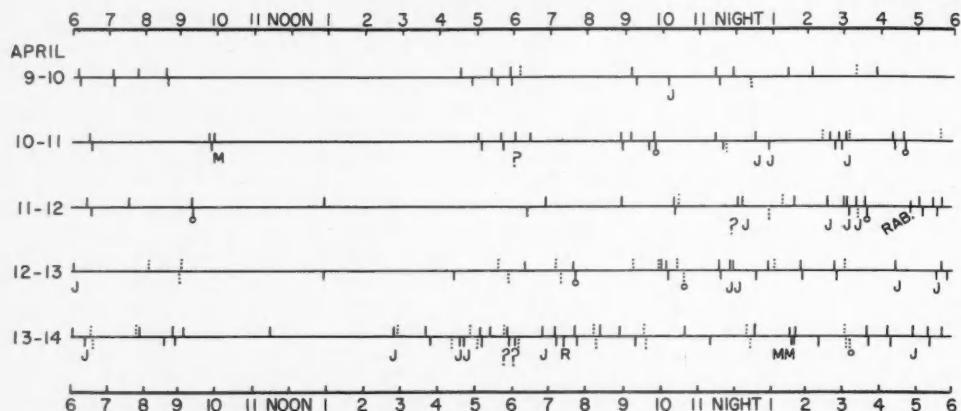


FIG. 19. A complete account of the traffic at Site SSI for 5 days. Short lines projecting above the base lines represent passages toward the left, lines below the base lines represent passages toward the right. Most of the traffic is by adult male M51 (solid, unlettered projections) and by adult, pregnant female M58 (dotted, unlettered projections). Solid projections distinguished by a letter J underneath them represent passages by juveniles between 2 and 4 weeks of age. Three passages marked M were by unmarked adult meadow mice and four passages marked with a question mark represent passages by meadow mice whose pose or position in the photographs was such that I could not determine whether they were marked or unmarked individuals. Projections tipped by a small circle represent passages when a mouse was carrying vegetation. One brush rabbit (*Sylvilagus bachmani*), marked RAB, and one harvest mouse (R) also passed during these 5 days.

passage and direction of travel of all of the various individuals in the runway at Site SSI during a sample 5-day period in April, 1957, when the female was in advanced pregnancy.

The histories of five litters can be traced, and the ages in weeks of the litters at the time they disappeared from the records were: 10,24; 5,19,28,28,32; 15,26, > 42; 3,3,3; and 4, > 13, > 13.

BURSTS OF ACTIVITY

On three occasions single individuals were recorded unusually frequently in a short time. On one of these occasions an adult lactating female (M67) made 15 round trips past the recorder in 13 minutes. Five weeks later, on June 23, the same female made 18 round trips within 2 hours, 13 of the trips within 47 minutes. On both of these occasions the female was carrying stems or leaves on many of her return trips. Presumably, therefore, these excursions were to bring in nesting or food material. Many of the round trips lasted less than 15 seconds, and one, at the end of which she returned carrying a piece of grass, lasted only 4 seconds.

The third burst of activity was provided by an unmarked juvenile on June 29. This individual made 13 round trips in 53 minutes. It was not visibly carrying anything in its mouth on any of these trips.

CARRYING OF VEGETATION

Numerous photographs were obtained of meadow mice carrying vegetation in their mouth, almost always blades or stems of grasses such as wild oats (*Avena fatua*) or leaves of herbs such as *Rumex*.

Undoubtedly many instances of carrying were overlooked when the items were small or when they projected from the side of the mouth away from the camera. Juveniles of unknown sex, young males, adult males, and adult females were all recorded carrying vegetation. Judging from the appearance of the items carried it is thought that most of them were food rather than nest material. Mice were recorded carrying vegetation 66 times on 30 different days, and 60 of these records were during April, May, and June, the months when the maximum amount of green vegetation was available. One "carrying passage" was recorded in January, one in August, and four in July. Carrying usually occurred between 4 and 9 a.m.

On five occasions an adult *Microtus* provided a flurry of carrying passages at some time within two days of the appearance of a new litter of young in the same runway. On three of these occasions the active mouse was known to be a lactating female, and on the other two the sex was unknown. It seems probable that the mother gathers a supply of cuttings at about the time the young are being weaned.

SUMMARY

Automatic cameras that recorded the traffic in runways of *Microtus californicus* over a period of 19 months revealed that on the average there were 7.8 passages by *Microtus* per runway per 24 hours. The greatest number was 67. During any one period of a few days the number of *Microtus* using one runway averaged about 6 and ranged from about 2 to 12. Runways with much traffic were not used by more

mice than runways with moderate traffic, and traffic was not noticeably greater in active runways when the population density was high. Traffic was slightly greater on moonless than on full-moon nights and, within the rainy season, was greater on rainy than on rainless days. The average male used the runways more frequently than the average female, and this was true in both the rainy and dry seasons.

Microtus californicus is primarily subterranean in habit and makes brief excursions out into the runways. The average duration of these excursions was 5 minutes. Daytime excursions lasted longer than those at night, and those by females lasted longer than those by males. Two individuals for which rather complete records are available averaged 3.0 and 3.2 excursions per day into the runway that was being recorded. Their average emerged times were 30 and 16 minutes per 24 hours. Three other individuals averaged 5.3 excursions per day. One individual that lived at least 32 weeks completed at least 612 excursions during his life and spent a total of at least 36 hours out in the runways. No short term rhythm of activity, as has been demonstrated for captive mierotines, could be noticed.

Mice were active at all hours of the day and night during the autumn, winter, and spring, but during the summer most of the activity was in the four hours following sunrise with smaller peaks of activity shortly before sunset and in the middle of the night. The summer activity pattern was not controlled by light, temperature, or by evaporation, but was probably determined by the availability of dew early in the morning. Mice of different ages and sexes showed the same activity pattern.

There was very little interchange of mice between two recording sites, even when the sites were only 5 meters apart, but several mice permanently moved their home ranges.

A male, a female, and their offspring shared the same runway without evidence that the female drove the male away or that the parents drove the young from the runway.

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POPULATION STRUCTURE AND DYNAMICS OF THE WESTERN SPOTTED
FROG, *RANA P. PRETIOSA* BAIRD & GIRARD,
IN YELLOWSTONE PARK, WYOMING

FREDERICK B. TURNER

*Museum of Vertebrate Zoology, University of California, Berkeley, California**

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INTRODUCTION

The western spotted frog, *Rana p. pretiosa*, has been studied only casually and our knowledge of its ecology has been based largely upon incidental reports, most of which have been summarized by Stebbins (1951). Basic quantitative data relating to the behavior of natural populations of this frog are lacking. In fact it has been only within the past few years that the structure and dynamics of *any* anuran populations have been investigated. Data from such studies are sorely needed, for our knowledge of vertebrate population ecology is based almost exclusively on studies of fish, birds and mammals.

There are a number of facets of anuran population ecology which seem susceptible to simultaneous study. One of these is the individual growth rate which, while of considerable interest in its own right, is also an important adjunct to the analysis of other problems. It is becoming increasingly evident that the rate of growth of anurans is not fixed but may vary between populations of the same species. And such variation is accompanied by differences in the age at which sexual maturity is attained. Thus, an expression of rate of growth and sexual maturation in any previously unstudied anuran population is likely to be of value. In the past, growth rates in various anuran species have been worked out by numerous authors but these data have rarely been utilized as a basis for the analysis of the age com-

position of the population in question. Marked fluctuations in the year-to-year age distribution of anuran populations might be expected but to what extent these occur is not yet known. The meager data available from former studies suggest that some populations, existing under stable conditions, may display a relatively fixed age distribution (e.g. Bannikov 1950) but that others may exhibit considerable fluctuation (e.g. Martof 1956b).

The survival rate in anuran populations has been appraised only rarely in the past. As a matter of fact it is not surely known whether postmetamorphic survival is relatively constant or whether certain age groups bear the brunt of mortality. Furthermore, the causes of mortality, whether predation or other factors, are notably unclear in the case of anuran populations. Quantitative data on larval mortality rates are virtually non-existent, despite the plea of Deevey (1947) for the direction of more attention to the survival of larval forms.

Previous studies of anuran movements have been primarily concerned with their magnitude, although some data have been presented pertaining to migrations and homing tendencies. No attempt has been made to interpret the dispersion patterns of anuran populations in terms of an annual cycle correlated with breeding activity, precipitation, and temperature. Nor do we know, except in a few cases (e.g. Fitch 1956), whether there are differences in vagility associated with differences in age and sex. Knowledge of the spatial requirements of anurans is scant, and

* Present Address: Department of Biology, Wayne State University, Detroit 2, Michigan.

rarely have data derived from studies of movements been analyzed so as to permit the quantitative definition of a home or activity range (e.g. Pearson 1955).

During the summers of 1953-1956 a study of the western spotted frog in a relatively undisturbed area in Yellowstone National Park, Wyoming, was carried out. I attempted to obtain data to elucidate the problems set forth above. Most of the field work was carried out during 1953, 1954, and 1955. The population studied, henceforth designated as the Lake Lodge Population, is located on the north shore of Yellowstone Lake and is adjacent, in part, to Lake Lodge, a commercial development of the Yellowstone Park Company. This population was the basis for a 3-year marking study and (except for the marking) was permitted to exist naturally throughout the study. The research was carried out while the writer was employed by the United States National Park Service and was approved by the Chief Park Naturalist, David deL. Condon, and by the Director of Region 2 of the United States National Park Service, Howard Baker.

It is a pleasure to acknowledge the cooperation of David deL. Condon, Chief Park Naturalist, as well as other Park Service personnel, without which this study could not have been carried out. I also wish to acknowledge the role of the Department of Zoology and the Museum of Vertebrate Zoology of the University of California at Berkeley in making available equipment and facilities instrumental in effecting the collection and analysis of data. The suggestions and criticisms of Dr. Robert C. Stebbins, Dr. Frank A. Pitelka, Dr. Edward S. Deevey, and Dr. Joseph G. Hickey pertaining to the preparation of the manuscript are gratefully acknowledged. Finally I want to express my particular appreciation to the numerous individuals who assisted me in various ways during the course of the field work. My wife, Mabel, and my brother, Lewis, contributed many hours of their time in this capacity. Among others who assisted were Dr. Ray Davis, Howard Haines, and William T. Daniel.

DESCRIPTION OF THE STUDY AREA

PHYSIOGRAPHY AND VEGETATION

The Lake Lodge study area, embracing the entire course and portions of the drainage of Soldier Creek including the springs from which it arises, is approximately 180 acres in extent and lies on the north shore of Yellowstone Lake near the outlet of the Yellowstone River (Fig. 1). As this area was too large to study intensively in its entirety, observations were concentrated in a tract of about 70 acres.

From Yellowstone Lake, at an elevation of 7731 ft above sea level, the area rises gradually to an elevation of about 7850 ft along its northern boundary. Soldier Creek (Fig. 2) is the only permanent water course in the area. This creek is fed by two springs, which are located in the northwestern portion of the area under observation. In the vicinity of the springs

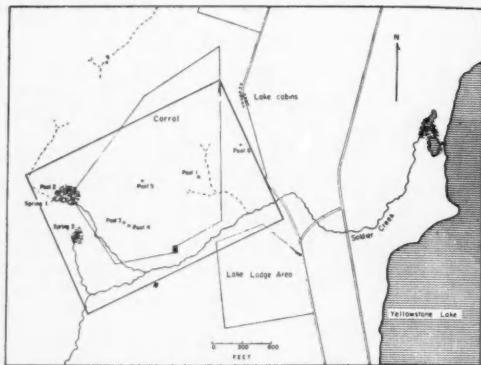


FIG. 1. The Lake Lodge study area, Yellowstone Park, Wyoming, showing the location of principal features; the rectangle encloses the 70 acres most intensively studied.

there are open, wet areas grown predominantly with sedges (*Carex* spp.), *Senecio sara*, *Mimulus guttatus*, *Arabis* sp., and *Veronica* sp. In the early autumn the springs and the water running from them may constitute the only water in the area though in some seasons one or two pools may persist until the first snows of fall. During the spring numerous ponds form and certain portions of the area are partly inundated. At this time Soldier Creek is fed by several more or less well-defined streams which are des-



FIG. 2. Soldier Creek, June 7, 1955.

tined to disappear later in the summer. The pools and flooded areas, stemming from melting snow and rain, are usually dry by early July but some of the former may persist throughout the summer. At the periphery of the rain pools, sedges, *Eleocharis* sp., *Rorippa* sp., *Polygonum* sp., *Geum macrophyllum*,

and *Pedicularis bracteosa* may occur (the last two in shaded situations).

The vegetational cover of the area as a whole may be generally described as an even-age lodgepole pine (*Pinus contorta*) forest, perhaps 100 years old. The understory is made up of pine seedlings, huckleberry (*Vaccinium scoparum*), occasional junipers (*Juniperus communis*) as well as numerous annuals and grasses. In riparian situations the pines may approach the stream closely but the understory is markedly modified. Here *Senecio* sp., *Mertensia* sp., and *Carex* spp. dominate.

The western chorus frog (*Pseudacris nigrita triseriata*) is common in the study area and utilizes, in general, the same breeding sites as *Rana pretiosa*. The western toad (*Bufo b. boreas*) is another amphibian present in the area but there is no evidence that it breeds in the same pools as the two other anurans. During most of the summer, from early June to September, horses (and sometimes mules) are run in a corral that occupies about 45 acres. The corral represents the most serious human infringement on the area, which is otherwise subject to minimal human use. A trail utilized by the National Park Service for daily guided walks during the summer traverses the area for a distance of about 800 yards. Soldier Creek flows immediately behind some of the Lake Lodge cabins, but since it passes through a small ravine over this portion of its course it rarely attracts the attention of visitors.

Certain features of the study area will be referred to with such frequency that it has been deemed convenient to designate them by numbers. The location of these features is indicated in Fig. 1 and a detailed discussion of them follows:

Pool 1: This pool forms in an open meadow from rain and melting snow during early May. At this time it is about 60 ft long and 45-50 ft in maximum width with a maximal depth of about 16 in. (Fig. 3). An aquatic plant, *Callitricha palustris*, grows at the surface of the pool during part of the month of June. Probably because of its exposed location, Pool 1 exhibits marked fluctuations in temperature with variations of as much as 13.3°C during a 24-hr period. As the summer advances Pool 1 becomes smaller until it finally disappears altogether. The pool was entirely dry by July 1, 1953, July 26, 1954, and July 12, 1955. It was dry on July 22, 1956, and apparently had been so for some days.

Pool 2: This pool is actually a spring located in what has been designated the Spring 1 Area. The pool is roughly elliptical with axes of approximately 4 and 10 ft. The greatest depths of this pool could not be determined because of the presence of a log in the water but measured depths varied from 2 to 3 ft. A dense growth of two species of *Spirogyra* clogs this spring. Pool 2 is surrounded by a somewhat boggy clearing grown predominantly with sedges. The water at the surface of the pool varies in temperature and a minimal temperature of 6.7°C and a



FIG. 3. Pool 1, June 7, 1955.

maximal temperature of 17.8°C were recorded at different times over a period of 2 years.

Pool 3: This is a pond which, like Pool 1, forms in May and is at that time about 40 × 60 ft with a maximum depth of about 14 in. Though the pool is located in an opening, lodgepole pines stand in fairly close proximity and shade the eastern half of the pool more or less completely. *Callitricha palustris* and an aquatic *Ranunculus* occur in the pool during late June and part of July but disappear later in the summer. Pool 3 exhibits a smaller range of variation in maximum and minimum temperatures than Pool 1 and is, in comparison with Pool 1, cooler during the day and slightly warmer at night. Pool 3 persists longer during the summer than Pool 1 and there was still water at the site of Pool 3 on September 20, 1954. However, Pool 3 had evaporated entirely by September 7, 1955.

Pool 4: Pool 4 forms from rain and melting snow during May and has a maximum length of 80 ft and widths ranging from about 12 to 28 ft. It has a maximum depth of about 1 ft. This pool is heavily shaded by lodgepole pines and supports little or no aquatic growth. Four fallen lodgepole pine snags in varying stages of decay lie wholly or partially in the pool, subdividing it more or less completely. Pool 4 is consistently colder than Pool 3 (except in May when both pools are clogged with melting snow). In 1954 Pool 4 was dry by August 22 and in 1955 by August 23.

Spring 1: There are a number of springs and seeps giving rise to the main branch of Soldier Creek. This area is generally boggy and grown only with sedges and a few herbs.

Spring 2: These springs give rise to the other branch of Soldier Creek. The vegetation and extent of this area are quite similar to that of Spring 1.

TEMPERATURE AND PRECIPITATION

The study area has a mean annual temperature of only 0.1°C and an annual mean precipitation of 19.97 in. The mean monthly temperatures are typical

of a continental climate, with a low of -11.7°C in January and a high of 13.4°C in July. The total precipitation is well-distributed over the year, ranging from a low of 1.37 inches in September to a high of 2.07 inches in January and March. Of greatest significance, insofar as this study is concerned, are the mean precipitation values for the summer months, i.e. the months during which *Rana p. pretiosa* is active. These values are as follows: May - 1.93 in., June - 2.01 in., July - 1.66 in., August - 1.41 in., and September - 1.37 in.

METHODS OF STUDY

Rana p. pretiosa is relatively easy to catch, either with a net or with the hands. Field work, involving the capture and marking of these frogs, was carried out from June 21 until September 11, 1953; May 21 until September 20, 1954; May 21 until September 6, 1955; on July 22 and 24, 1956, and August 13, 1959. Frogs were marked by clipping toes in various patterns, and a small spring-type fingernail clipper was used for this purpose. The thumbs were not excised and normally no more than two digits were removed from any one hand or foot. Regeneration was slow and apparently limited so that digits removed in 1953 were still absent in 1959. Because digits may be lost under normal conditions of existence, questions sometimes arose as to the identity of frogs. Records of size and sex made at the time of marking usually resolved such problems. Measurements were made in 1953 by placing a millimeter scale along the back of the frog to be measured and recording the snout-vent length to the nearest millimeter. In 1954, 1955, 1956, and 1959, a pair of steel calipers was adjusted to the above-mentioned dimension and transferred to a millimeter scale. These measurements were recorded to the nearest half-millimeter. The frogs, when measured, were held in the palm of the left hand. If the frog's back appeared strongly arched an effort was made to induce a more normal posture before the measurement was made. Usually frogs sat quietly while measured; if they jumped, repeated handling seemed finally to induce the necessary quiescence. Occasionally particularly active frogs were subdued by rapping them sharply on the head with the arms of the calipers. These frogs were stunned long enough to enable the measurement to be made. The sex of the frog, if it could be recognized, was recorded. In contrast to the technique of Ryan (1953) and Hamilton (1955), who made three measurements to obtain an average value, a single measurement was taken in this study. It must be admitted that multiple measurements are more accurate but it is felt that the shortcomings of the study in this respect are compensated by the larger number of measurements.

The determination of the sex of living *Rana p. pretiosa* is sometimes an uncertain procedure, especially in the case of younger individuals. The presence of black callosities on the thumbs of the males

was found to be the best single criterion for sex determination, although the quality of croaking (if it occurred) and the size and build of the frog were also of value.

Numbers of eggs were estimated by means of a volumetric analysis. Following a comparison of the number of eggs (determined by actual count) in egg masses of known volume, it was assumed that each egg mass contained 1.4 eggs (Turner 1958).

The point of original capture of every unmarked frog, as well as points at which recaptures of marked frogs occurred, were recorded on maps of the study area. A new map was used for each field trip. The time of day and air and water temperatures were recorded at each general locality where frogs were taken. Temperatures were taken with a quick-registering Centigrade thermometer. Some of the water temperatures obtained in 1954 were recorded by TAG (No. 13553) recording thermometers with 7-day chart drive mechanisms. Long-range records of precipitation and temperature, as well as similar records for the summers of 1953-55, were obtained from Lake Ranger Station, which is located about one mile from the study area.

INDIVIDUAL GROWTH RATE

Metamorphosed frogs were collected at random throughout the study. Unmarked frogs were measured and marked as they were captured and then released at the point of capture. Marked frogs which were recaptured were usually remeasured. A total of 1433 original measurements (all but 159 during 1954 and 1955) and 768 subsequent remeasurements (all during 1954, 1955, 1956 and 1959) were made. The 768 remeasurements involved 391 frogs, or about 27% of the total number of measured individuals.

GROWTH BETWEEN TRANSFORMATION AND FIRST HIBERNATION

It is evident that the amount of growth between the time of transformation and the first hibernation will depend primarily on the time which elapses between these two events. Hence frogs which transform relatively early in a summer season may be expected to be the larger members of the first year-class which emerges the following spring. In general, the size limits of this year-class will reflect differences in the time at which its members transformed and hibernated. Furthermore, the first year-class may be slightly augmented after its emergence by newly transformed frogs which did not transform during the preceding summer.

As a result, the first year-class, upon emergence in May, exhibits a range in size from 20 to 30 mm with a mean of 25 mm (the method by which these values were determined is explained later). Since the mean transformation size is about 16 mm the average growth between transformation and hibernation may be expressed as approximately 9 mm.

GROWTH DURING THE FIRST 5 YEARS

Attention may now be turned to the rate of growth during the first full year (and subsequent years) following transformation. In the discussion which follows the first year-class is considered to be those frogs in their first *full* season following transformation and older year-classes are designated accordingly.

In working out a hypothesis to interpret the data which follow, two attributes of the population have been considered: the size limits (20-72 mm) and the relative size of males and females. Apparently the maximum size attained by the females is about 70 mm while the largest males are around 60 mm in length. In many species of anurans the females are larger than the males, a condition existing in *Rana pretiosa*. This phenomenon could be an expression of greater longevity in females or, as is generally assumed, of differential growth rates of the sexes, or perhaps a combination of both factors. At any rate, a hypothesis pertaining to rates of growth in the population under study must take into consideration this disparity of adult sizes.

Records of 45 frogs for which at least four significant (i.e. at least one week apart) measurements existed were used both as a basis for the approximation of growth rate, and as the ingredients of a model analysis which could be expanded to incorporate the entire series of growth measurements. In order to illustrate the analytical procedure the measurements of 22 frogs are presented in Table 1. Each annual growth period (which has been assumed to be May 15-September 15) has been broken up into 8 sub-

divisions of approximately equal duration. The measurements for individual frogs have been entered in appropriate columns and assigned to year-classes. When two or more measurements have been recorded during one two-week period a mean value has been substituted.

The model in Table 1 has not been extended beyond the 5th year-class because by the time this age is attained the annual growth rate is so slow that it is impossible to designate age with certainty. Consequently, the following remarks pertain specifically to growth during the first 5 years after transformation.

The mode of analysis is equally applicable to frogs for which less than 4 significant measurements exist. Consequently the remaining frogs, for which only 2 or 3 measurements were available, were treated in a similar manner. Furthermore, it was decided that the study could be reinforced by including the single measurements of frogs which were never re-measured. This last procedure differs little from an arbitrary designation of age on the basis of size but it must be borne in mind that the model was available as a guide. It was recognized that the year-class assignment of any frog measured but once, depended not only on its size but also the time of season at which the frog was measured. Because young frogs show appreciable growth in the course of a growing season, it was necessary to keep clearly in mind the approximate size-limits of each of the first 3 year-classes as the frogs grew throughout the summer. The manner in which the size limits of the

TABLE 1. Analysis of growth of 22 selected *Rana p. pretiosa* from the Lake Lodge population, illustrating year-class assignment and growth during the first 4½ growing seasons after transformation. All sizes in mm. The 8 subdivisions of the growing seasons represent the following time periods: (1) May 21-31, (2) June 1-15, (3) June 16-30, (4) July 1-15, (5) July 16-31, (6) August 1-15, (7) August 16-31, (8) September 1-20.

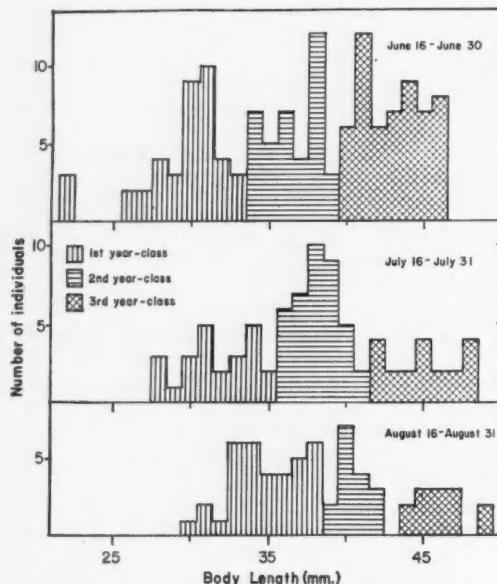


FIG. 4. Size distribution of *Rana p. pretiosa* 1 to 3 yrs. of age collected in the Lake Lodge population during 3 different periods of the season (1953, 1954, and 1955 combined). The manner in which the limits of the first three yr-classes were revised in accordance with estimated growth is indicated.

first three year-classes were revised as the season advanced is illustrated in Fig. 4.

The sex of members of the 4th and 5th year-classes could usually be distinguished, so data pertaining to males and females of these ages were treated separately. The mean sizes of males of the 4th and 5th year-classes were found to be consistently less than those of females of the same age, but no statistically significant size differences between the sexes could be demonstrated. The results of the entire analytical procedure are tabulated in Table 2 and depicted graphically in Fig. 5. Mean values (for males and females combined) are used for the 4th and 5th year-classes; these values have been derived from all of the measurements recorded for each of the 8 fifteen-day periods during the first 5 growing seasons.

GROWTH AFTER THE ATTAINMENT OF 5 YEARS OF AGE

The difficulty in evaluating later growth has already been mentioned, but because a large amount of data pertained to frogs more than 5 years old I have extended the analysis to include older frogs, even though certain assumptions which are not entirely valid are involved. The difficulty lies in the fact that in older frogs individual differences in growth rate may become sufficiently magnified so as to preclude any definite correlation between age and body length. Data collected on August 13, 1959, throw some light on this problem. At this time, 63 frogs were collected,

TABLE 2. Analysis of growth rate of *Rana p. pretiosa* in the Lake Lodge population during the first 5 years following transformation. All sizes in mm. The eight subdivisions of the summer are as in Table 1.

Year-class and total range in size		TIME OF SUMMER							
		1	2	3	4	5	6	7	8
1 (20-38)	N	38	21	61	48	59	153	55	43
	Mean size	25	27	28	28½	32½	33	35	35
2 (28-44)	N	10	31	72	103	67	31	24	29
	Mean size	34	34	35½	35½	38½	39½	40	40½
3 (37-49)	N	13	50	89	68	29	51	29	11
	Mean size	40½	41	42½	43	45	45½	46	46½
4 (45-54)	N	14	29	43	43	14	22	14	11
	Mean size	47½	47	48	48	49½	50	50	50
5 (47-55)	N	21	41	42	30	7	15	7	6
	Mean size	50	50½	51	51½	52	52	52½	52½

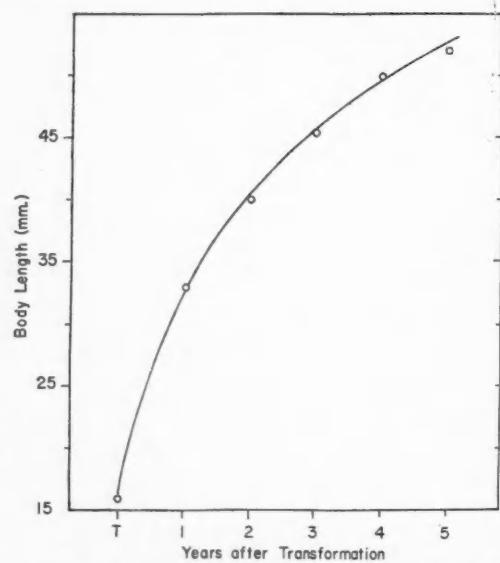


FIG. 5. Mean rate of individual growth in the Lake Lodge population of *Rana p. pretiosa* during the first 5 yrs after transformation. Size at transformation (T) and in August of successive years is illustrated.

13 of which were marked. The size and sex of 10 of the 13 marked frogs could be reasonably reconciled with the original marking data of 1953-55. These frogs were 1-4 yrs old when marked and ranged from 6 to 8 yrs old when recaptured in 1959. These records, then, permit a tentative extrapolation of growth beyond the 5th year. In Table 3 the ages of 117, 350, 215, 722 (males), and 601, 1527, 1532,

1212, 1303, 1393 (females) are known; the ages of the others are estimated. No attempt has been made to subdivide the annual growth increment of these older frogs. It is evident from Table 3 that males grow slowly after they are 5 or 6 yrs old. Measurements of the same individual in 3 consecutive years (e.g. 8, 134, 51) show hardly any change. The largest male measured in the population was 61 mm in length. Females grow fairly rapidly up to about 60 mm. This size may be attained as early as 6 years (601, 1532) but ordinarily at least a year later (1212, 1393, 1303, 1527). Measurements of females more than 60 mm in length in the course of 3 different seasons do not show much change (e.g. 41, 122, 99). The largest female measured was 72 mm.

TABLE 3. Postulated growth in 6th and subsequent years after transformation in male (above) and female (below) *Rana p. pretiosa* from the Lake Lodge population. The ages of 117, 350, 215, 722 (males) and 601, 1527, 1532, 1212, 1303, 1393 (females) are known, and serve as the basis for estimates. Sizes (in mm) for all year-classes are averages of all measurements taken during the same year.

Male Frog No.	YEAR-CLASS										
	1	2	3	4	5	6	7	8	9	10	11
117.....	30					54					
350.....	28				54						
215.....		36				54					
722.....			42				55				
436.....				48	51	53					
464.....				47	48	49					
5.....					50	50½	54½				
8.....							55	56	56		
134.....							55	55½	56½		
51.....							58	57	57½		
Female Frog No.											
601.....	27					60					
1527.....		39				56					
1532.....		36				60					
1212.....		38					58				
1303.....		34				55					
1393.....			47½				61				
718.....			49	50½							
160.....					56½	57					
77.....					54	56½	60				
42.....					56	59½	62				
41.....						60	61	61			
122.....						60	61½	63			
99.....							64	64	64½		
102.....							65	66	69		

The conservative interpretation of these data would be that the largest males and females are simply those which have grown most rapidly. Thus a male 57 mm or more might be, say, only 8 or 9 years old. The largest females, around 70 mm, might be only 9 or 10 years old (it is hard to imagine the attainment of such a size any sooner). This conservative view is expressed in Table 3. It is, however, possible to interpret the data as indicating a maximal longevity of about 10 years in males and 12 to 13 years in females.

While it is true that such longevity is unusual in view of what is generally known of anuran life histories, there are aspects of the foregoing data which can hardly be reconciled with classical concepts. Certainly the pattern of growth during the first five years following transformation (Fig. 5) is well-defined. Indeed, Force (1933) has shown that *Rana pipiens* in Michigan grows at a comparable rate during the first four years after transformation. Furthermore, the growth of larger *Rana pretiosa* is only a few millimeters a year—or even hardly perceptible in the largest individuals (Table 3). To account for the presence in the population of a 61 mm male and a 72 mm female by an extrapolation of the growth curve in Fig. 7, one must postulate a maximal life-span on the order of 10 years.

ATTAINMENT OF SEXUAL MATURITY

On the basis of the age composition of breeding aggregations during late May and early June I have concluded that males breed for the first time at the beginning of their 4th year, or at an age of about 3 years and 9 months. Females apparently do not breed until the beginning of their 5th or 6th year. Whether the frogs may actually come to maturity some time during the middle or late summer prior to the season of first breeding activity is not known. In all other anurans so far studied the attainment of sexual maturity is much earlier in life—by the end of the season of transformation in some forms. The protraction of pre-reproductive life in the Lake Lodge population of *Rana p. pretiosa* is a corollary of the slow growth and long life-span of these frogs.

SEASONAL RATE OF GROWTH

Growth curves as in Fig. 5 are useful representations of average growth over a period of years, but whereas such curves usually illustrate a progressive decline in successive annual growth increments, they give no indication of variation in rate during any one season. Such variation almost certainly occurs in all anurans whether the annual cycle is continuous or interrupted by periods of dormancy. The work of Ryan (1953) and Martof (1956a) with *Rana clamitans* and of Fitch (1956) with *Gastrophryne olivacea* has shed considerable light, in a quantitative sense, on this problem in these two species. Martof demonstrated that the seasonal growth curve of *Rana clamitans* in Michigan is sigmoid, with maximal growth occurring during June, July, and August. In general, this pattern is exhibited by other species which have been studied in detail. However, Ryan reported that in large green frogs (80+ mm) the little growth which does occur takes place from mid-May until the end of June.

Seasonal growth rates (for 5 years) in the population of *Rana pretiosa* under study is illustrated in Fig. 6. From this figure it is apparent that, at least during the first four years after transformation, the most vigorous growth occurs in July. The data do not permit any conclusions pertaining to variation

in growth rates during a single season in older frogs. My opinion is that the larger frogs exhibit their maximal growth during the same period of time as do the younger individuals.

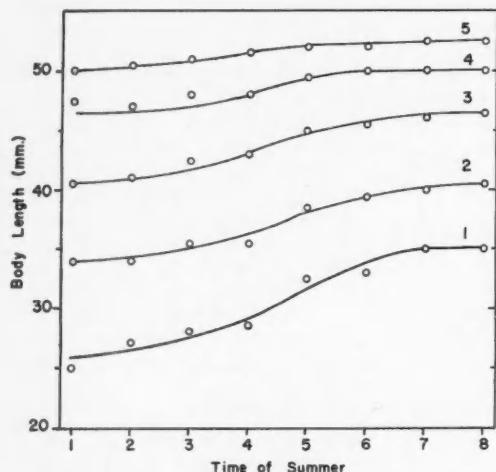


FIG. 6. Seasonal rate of growth of *Rana p. pretiosa* during the first 5 yrs after transformation. The 8 subdivisions of the summer are as in Table 1.

DIFFERENTIAL GROWTH OF THE SEXES

As has been mentioned earlier, the structure of the population studied strongly suggests a more rapid rate of growth in females. This is true of *Rana catesbeiana* (Raney & Ingram 1941), *Gastrophryne olivacea* (Fitch 1956), at least some populations of *Rana clamitans* (Ryan 1953) and probably is so in other anuran species exhibiting size dimorphism (with the females larger). Differential mortality of old males and females may be involved in some cases, but that such structural attributes of populations may be simply due to differential growth rates has been demonstrated by Pearson (1955) with *Scaphiopus h. holbrookii* in Florida. In this species the males are larger. There are two aspects of this condition deserving attention: the amount of difference in the maximal sizes of the sexes and the manner in which this difference arises.

Ryan (1953) found that female green frogs in New York averaged about 65 mm and males 60 mm by the time they were 1 yr old. The largest females were about 98 mm and the largest males around 90 mm in length. This difference apparently builds up gradually and is manifested as early as the season in which transformation occurs. However, Martof (1956a) found no marked difference in the growth rates of male and female *Rana clamitans* in Michigan. Fitch (1956) has shown that there are clear differences in the size of the sexes in *Gastrophryne olivacea* by the second full year following transformation. The data of Raney & Ingram (1941) show only small differences (ca. 2 mm) in the average size of male and

female bullfrogs even in the third and fourth summers after transformation, although ultimately the females exceed the males considerably in size.

In the population of *Rana pretiosa* studied the size difference seems to arise gradually, but the time at which it is first manifest is uncertain. It has already been pointed out that what appear to be size differences in the fourth and fifth year males and females are not statistically significant. Still I feel that the divergence, which is destined to produce a difference of approximately 10 mm in the maximal size of males and females, is initiated during the fourth year. In general the expression of a size difference between the sexes in *Rana pretiosa* in Yellowstone Park is retarded when compared to other anurans studied.

INDIVIDUAL VARIATION IN GROWTH RATE

Variation in the growth rate of different individuals, apart from sex differences, is an attribute of all animals. Among anurans the least variation appears in Hamilton's (1934) toads. His data pertain, with perhaps one exception, to the growth of toads during the first year after transformation. The measurements are few, but show a rather uniform growth rate for the individuals involved. A fair degree of uniformity in *Rana catesbeiana* is reflected by the data of Raney & Ingram (1941), but it is stated that the faster growing females reach their approximate maximum size in 2 yrs after maturity (i.e. in the fourth full year after transformation) while the females showing the slowest growth would reach this stage in 3 or 4 years (i.e. 5 or 6 years after transformation). Some males are presumed to attain maximal size 2 or 3 years after maturity so there is an implication of comparable variation in this sex.

In *Rana pretiosa* it was found that there was some overlap of the year-class size limits. Part of this is apparently independent of slight differences in age due to time of transformation. For example, one measurement of a frog may be perfectly "in phase" with the population and a successive one inexplicably high or low. There were cases of unusually slow growth where frogs only 2 or 3 yrs of age registered either no growth or only a millimeter or so of growth in the course of a year. On the other hand one 2-yr old grew 12 mm in 10 weeks and there were other cases involving frogs of all ages where growth was comparably accelerated. Particular effort was made to rule out the possibility of misidentifications but error in measurements could be involved in some of this apparently aberrant growth.

LOSS OF LENGTH

In this study of *Rana pretiosa* 92 measurements suggested loss of length. The average magnitude of apparent loss (ca. 1 mm) is approximately the same regardless of the size of the frogs involved and hence the per cent of error in measurements is highest in the case of small frogs. Presumably these measure-

ments are owing to some technical error in the system of measurement employed. But Raney & Lachner (1947) have suggested that "Another possible explanation assumes an actual loss of length due to a possible harmful effect of the tag which may have interfered with normal feeding in some. Or it may be that the longest and oldest toads actually shrink in length." In this study of *Rana pretiosa* most of the cases of measured loss of length involve an initial measurement in May or early June and a subsequent measurement later in the season. This is probably due to the fact that the slow growth rate in the first month after emergence permits variation in measurements to be revealed, while the accelerated growth later in the season would tend to conceal these inexactitudes. An alternate explanation might postulate an actual loss of length associated in some way with breeding activities but since the body measurements were based on a skeletal dimension it is hard to explain how this could occur.

STRUCTURE OF THE LAKE LODGE POPULATION

The sex ratio and age structure of natural populations and the changes which these attributes may undergo because of variation in reproductive success and/or rate of survival have been accorded more and more attention in recent years. The genetic and evolutionary implications of such fluctuations, vigorously propounded by Wright (1940) and Dobzhansky (1941), are now given considerable attention in attempting to interpret the dynamics of natural populations. As has been pointed out by Jameson (1955), groups other than the Amphibia have been subjected to the most intensive study in these respects, but the work of Bannikov (1949, 1950), Jameson (1955), Pearson (1955), and Martof (1956b) indicates that amphibians are susceptible to similar investigations.

SEX RATIO

Between 1953 and 1955, 199 male and 400 female frogs 45 mm or more in length were marked in the Lake Lodge population. After frogs of uncertain age were eliminated from the samples there remained 169 males and 309 females for consideration. The age composition of this total of 478 frogs is presented in Table 4. It may be observed that a sex ratio of roughly 1:1 exists until the fifth

TABLE 4. Male:female ratios in 478 *Rana p. pretiosa* four years and older from the Lake Lodge population, Yellowstone Park, Wyoming. Figures represent frogs of each age group newly marked in each of 3 years.

	1953	1954	1955	Totals
4th year frogs	14:11	35:42	13:7	62:60
5th year frogs	11:13	37:35	4:8	52:56
older frogs...	18:64	28:101	9:28	55:193

year. The number of males and females 6 years of age and older indicates that either older males are for some reason less prone to capture or that they are actually fewer in number.

Almost all previous work pertaining to the sex ratio in the genus *Rana* has revealed a preponderance of females. Thus, the early work of European investigators with *Rana temporaria* and *R. esculenta*, summarized by Pelseneer (1926), show that females may make up from 53% to about 62% of samples of these frogs. Balli (1938) examined large samples of *R. esculenta* and found that of 5225 frogs of all ages from three different populations there were 1828 males (35%) and 3397 females (65%). Martof (1956b) found that female *R. clamitans* made up 56% of a sample of 389 frogs, but this was not a significant departure from a 1:1 ratio.

The overall percentage of female *R. pretiosa* in the sample of 478 frogs from the Lake Lodge population was about 65%, which happens to coincide almost exactly with Balli's findings in *R. esculenta* (the proportion of adult females was 66%). However, in *R. pretiosa* the apparent preponderance of females does not arise until 5 years after transformation while in *R. esculenta* proportions of *juvenile* males and females were, on the whole, identical with those of the adults. This implies a different rate of survival for male and female *R. esculenta* almost from the time of transformation. Or, as is quite likely, it may be simply that some of the juvenile "females" are destined to become males—a condition which seems to exist in *R. temporaria*. Goldschmidt (1923) reviews the earlier work of Hertwig and Witschi with populations of *R. temporaria* in Germany where it was found that some populations exhibit an apparent excess of females. However, over varying periods of time a proportion of these "females" become males so that the sex ratio of adult frogs is adjusted to 1:1.

While it cannot be stated with certainty that the older frogs in the Lake Lodge population are preponderantly females, this seems to me as reasonable an explanation of the age composition of the samples as the assumption that there was some persistent bias in sampling technique. Wills (1936) has shown that, in sexually mature *Taricha torosa*, males exhibit a higher rate of metabolic activity than females but the extent of this condition in the Amphibia is unknown. However, certain of my data indicate that most of the male *Rana pretiosa* breed every year while females do not—perhaps this is associated with a higher level of metabolic activity in males, at least during the breeding season. One should further consider the passive breeding behavior of females and the fact that when they do enter into mating activities they spend less time at breeding sites than males.

Rubner (1908) postulated a relationship between longevity and level of metabolic activity and, according to Pearl & Miner (1935), "The inverse

correlation between rate of living and duration of individual life has been demonstrated by a considerable body of recent experimental work on various forms . . . That rate of living is a major factor in determining longevity admits of no doubt." This suggests that there might be a somewhat higher mortality rate among older males. Hence the disparity in numbers of older males and females in the samples need not be automatically construed as a result of bias in sampling effort.

POST-METAMORPHIC AGE STRUCTURE AND SURVIVAL

It is difficult to work out the age composition of a population in which the growth of individuals is relatively slow and in which some individuals may live for a number of years. From the data developed with regard to individual growth rates, one would expect an appreciable proportion of the Lake Lodge population to be made up of older individuals, presenting a size frequency-distribution without apparent discontinuities. Such is indeed the case. While it is possible to define the size-limits of the first three year-classes with confidence (Fig. 4), and do a reasonable job of separating 4th- and 5th-year individuals, it is almost impossible to categorize older frogs (see above).

The age distribution of frogs marked in 1953, 1954, and 1955, and recaptured in 1954, 1955, and 1956, is indicated in Table 5. The data for 1953

TABLE 5. Age composition of samples of *Rana p. pretiosa* taken from the Lake Lodge population during 1953 (R_0), 1954 (u_1) and 1955 (u_2). Recapture data are indicated by the letter m and subscripts. Subscript 0 refers to 1953, 1 to 1954, 2 to 1955, and 3 to 1956. The first number of a subscript refers to the year originally marked; subsequent letters to years during which recaptures occurred.

Year-class	1953	1954	1955				1956				m ₁₃	m ₀₁₂₃	m ₁₂₃	m ₀₂₃	m ₃₂
	Ro	R ₁		R ₂		R ₃		m ₁₃	m ₀₁₂₃	m ₁₂₃	m ₀₂₃	m ₃₂			
1	52	25	333	4	10	112	22	3	1	4					
2	13	5	94	3	1	20	62	2							
3	46	14	106	2	6	38	38	2							
4C ^a	17	10	36	1	6	19	14				2				
4♀	16	5	42	4	3	11	8				1				
5C ^a	15	7	38	0	3	16	4								
5♀	22	12	35	2	4	20	9					1			
6+ σ^a	23	9	28	3	6	6	9								
6+♀	93	26	101	5	10	29	28					1			
Total	297	113	813	24	49	271	194	7	1	7	1	8			

and 1956 are not representative, for in 1953 a particular effort was made to catch adults, with the result that the older year-classes are disproportionately represented. Eighty-six frogs captured in 1953 were not measured and these have been prorated among the various age groups. The 1953 and 1956 data will be used in conjunction with estimates of survival and for this reason they have been included in Table 5.

Minimal survival between 1953-54 (38%) and 1954-55 (33%) may be easily calculated from the numbers of marked frogs recovered one year after marking. However, owing to emigration and the impossibility of capturing every marked frog present in the population, these data do not establish the absolute mortality rate. If we examine the 1954 and 1955 data (which probably represent the true proportions of the various age classes fairly closely), we may see that it would be highly undesirable to attempt to estimate survival by examining the age composition of the population for any given year —i.e. in the manner that one would prepare a vertical life table (Deevey 1947, Hickey 1952). The variable annual recruitment results in year-classes of irregular size, with some of the older groups exceeding younger generations in numbers (the very small first year-class in 1955 is a consequence of the poor reproductive success in 1954).

Assuming that the mortality is distributed evenly among the age groups, the survival rate (P) for the whole population may be estimated by means of the following formula:

$$P = \frac{m_{01}s_2 + u_1m_{02}}{m_{12}R_0}$$

This equation is derived by Leslie & Chitty (1951) and is applicable to a chain of 3 successive samplings (in this case the entire samples of 1953, 1954, and 1955) in which the marked animals recaptured at t_1 (1954) and t_2 (1955) are grouped according to the last time they were captured. The reader is referred to this paper for a fuller explanation and a treatment of the more general case of a series of n successive samples ($n > 3$). In the equation, because of grouping, m_{12} is equal to the sum of the m_{012} and m_{12} columns in Table 5. The 333 first-year frogs captured in 1954 have been excluded from the test (though including them changes the outcome only slightly), and hence u_1 is 480 (813 - 333) and m_{12} is 208 (271 + 49 - 112). The other values may be taken directly from Table 5. P is then estimated at .61 and the death (=mortality + emigration) rate (1-P) is .39. It is also possible to estimate the variance of P as follows (Leslie & Chitty 1951):

$$\text{Var}(P) = \frac{m_{02}s_2R_1^2}{m_{12}^3R_0^2}$$

This value is .002466, which gives a standard deviation of .05. These values apply only to the 1953-54 interval.

A check on this estimate of P may be obtained by a method proposed by Ricker (1945) for estimating mortality in fish. Let x be the number of animals marked and released in the first year (in this case 297) and let c be the recaptures in this group in the second year. Now if a group of animals has been marked and released at the beginning of the second year (y) and a number of these (d) are caught during the second year, the rate of exploitation (or the efficiency of recapture) during the second year is d/y . Between May 21 and June 4, 1954, 170 new frogs were marked (y). Ninety-eight of these were recaptured during 1954 after June 4.

$$(R_1 + R_2) - \left[\frac{u_1}{1 - R_0 X} + \frac{u_2}{1 - (R_0 + P^{-1}u_1)X} \right] = 0$$

This equation has been developed by Leslie (1952) and is applicable when the death-rate is constant over the period of sampling and there is no dilution (by births or immigration). Leslie points out that the assumption of a constant death-rate will be valid for a great deal of data, and, as will be seen, the death-rate between 1954-55 probably does not differ greatly from .39. Dilution in the population under study is primarily by newly transformed frogs (i.e. frogs of the first year-class). Since these individuals may be recognized and have been recorded, it is possible to simply exclude them from consideration. New frogs marked in 1954 (u_1) are then $813 - 333$ or 480 (and $R_1 = 480 + 113$). In 1955, 194 unmarked frogs were captured, 62 of which were 2 yrs old, and 22 one-yr old. Hence, u_2 is actually 110 ($194 - 62 - 22$). Similarly, the 112 first-yr frogs recaptured as 2-yr olds in 1955 must be excluded so $R_2 = u_2$ (110) plus 159 ($271 - 112$) + 73 (49 + 24) or 342. With these values, the equation yields a value of $X = .00063$ and hence $N_0 = 1587$.

The 1953 population size may also be estimated by use of the Lincoln (proportional) index. Then $N_0 = 297 \times 593/113$ or 1559. The variance of this estimate may be estimated as $\text{Var}(N_0) = 297^2 \times 593 \times 480/113^3$ or 17,400 (after Bailey 1952). The standard deviation is approximately 132.

Returning again to the Leslie estimate (which will be the estimate referred to in subsequent discussion), we may assume that the 1953 population was on the order of 1587 individuals, and that about 970 (61%) were present in 1954, the other 600-odd either dying or moving into other areas so as to be no longer at risk. This would imply that of the 297 frogs marked in 1953, 181 were present in 1954; of the 1290 unmarked frogs in 1953, 788 were present in 1954. The 1954 captures in these two categories, 113 and 480 respectively, are about in the same proportion to those presumed at risk ($113/181$

Of the 297 frogs marked in 1953 (x), 100 were recaptured during 1954 after June 4 (c). Knowing the efficiency of recapture ($d/y = 98/170$ or .58) we may calculate that there were actually on the order of 173 frogs marked in 1953 at large in 1954 ($100 \times 170/98$) and hence that the survival between 1953 and 1954 was .58 ($173/297$). This estimate is close to the estimate of survival (.61) arrived at by means of the first formula.

However, an advantage of using the first formula is that after P has been estimated, an estimate of N_0 (population size in 1953) may be obtained. This is done by solving the following equation by iteration (in which X is a parameter = $\frac{1}{N_0}$):

$$= .62 \text{ and } 480/788 = .61), \text{ and close to the recapture efficiency of .58 estimated by Ricker's method.}$$

We may now estimate the 1954 replacement, i.e. frogs which transformed at the end of the summer of 1953, and which I consider first-year frogs in 1954. If the efficiency of sampling in 1954 was on the order of .6, then the 333 first-year frogs marked in 1954 were actually representatives of a cohort of 555 ($333 \times 10/6$) which was added to the population as a result of the 1953 reproductive effort. Then in 1953-54 the population just about broke even, the mortality-emigration of about 600 being approximately offset by recruitment of young. There was undoubtedly some immigration of older frogs which cannot be assessed quantitatively.

The survival between 1954-55 can be crudely estimated by using the limited data obtained in July of 1956 (Table 5). Let us assume that 1954 was the first year of sampling. Then it is possible, by various recombinations, to estimate P by a three-point sampling (1954-55-56), this P pertaining to the interval 1954-55. The new values are: $R_0 = 926$ ($R_0 + m_{01}$); $m_{01} = 320$ ($m_{012} + m_{12}$); $u_1 = 196$ ($194 - 22 + 24$); $m_{02} = 6$ ($m_{13} + m_{013}$); $m_{12} = 18$ ($m_{0123} + m_{023} + m_{123} + m_{23}$) and $s_2 = 24$. This gives an estimate of $P = .53$ with a standard deviation of .09 and implies an efficiency of recapture of about .63 in 1955 ($271/813 \times .53$). When P is estimated by Ricker's method the value is .70 (with a recapture efficiency of .43). Because of the conflict in these estimates and because of the scantiness of the 1956 sample, changes in population size between 1954 and 1955 can be described only in general terms. Certainly we may expect a decline in numbers, roughly on the same order of magnitude as in the preceding year (if we adopt a value of P about midway between the Leslie & Chitty and the Ricker estimates). The significant point is that, regardless of the value of P , the recruitment in 1955 was negligible. The 22 first-yr frogs marked in

1955 may be considered representatives of a cohort of 35-50, depending on how effectively the population was actually sampled. The total population size then dropped rather abruptly in 1955, possibly to something on the order of 1000 individuals, with few first-yr frogs.

Let us now return to the question of the age-specific mortality rate. As has been pointed out, the successful application of the Leslie & Chitty (1951) equation depends on an age-constant mortality rate. Is such an assumption justified in this study? A rapid and rather uncritical appraisal of mortality among the different age groups may be made by comparing the 1955 recaptures of frogs of various ages marked in 1954. If one age group were suffering particularly heavy mortality, one would expect relatively fewer of its members marked in 1954 to be recaptured in 1955. Exactly $\frac{1}{3}$ of all of the frogs marked in 1954 were recaptured in 1955. The proportions of each age group recaptured are: 1 - .33 (112/333, etc.); 2 - .21; 3 - .36; 4 - .38; 5 - .49; 6+ - .27. In the absence of a test of the significance of these figures it may be stated that, except for the second and fifth year-classes, there are no drastic differences in the survival of the various age-groups. At any rate it is unlikely that the first year-class bears the brunt of the annual mortality.

It is possible to apply the equation of Leslie & Chitty to each age group, using data directly from Table 5, except for frogs 5 yrs of age and older. For example, in the case of the first-yr frogs, R_0 is 52, m_{01} is 25, u_1 is 94 (note that this value is the unmarked frogs 2 yrs old taken in 1954), m_{02} is 4, m_{12} is 30 (m_{012} for first-yr frogs plus m_{12} for second-yr frogs) and s_2 is 34 (total marked frogs captured at t_2). In the case of frogs 5 yrs of age or older, it was necessary to make an arbitrary separation of 6-yr old frogs and frogs considered 7 yrs of age or older from the u_1 and m_{12} columns in Table 5. The age specific P values estimated in this manner are recorded in Table 6. While these results are far from conclusive—one value (1.04) is impossible and at least one (.96) unreasonable, and in most cases the variances are large, due to a reduction in the numbers of animals involved and to the use of a 3-point sampling—they do not reveal any clear cut differences in age-specific mortality rates (using $\pm 1.96s$ as 95% fiducial limits). If the 4th-yr frogs of both sexes are combined, $P = .73$; if the 5th-yr frogs are combined, $P = .71$; and if frogs of 6 yrs or older are combined, $P = .49$. If all males in these groups are combined, $P = .61$; if all females are combined, $P = .54$. None of these P values differs significantly from any other. A survivorship curve based on the original calculation of P would, then, be of the diagonal type (Type II, as defined by Pearl & Miner 1935) for both sexes, and it would reflect an approximately constant mortality rate (ca. $.39 \pm .10$) throughout postmetamorphic life.

TABLE 6. Analysis of age-specific survival rate (P) in *Kana p. pretiosa*.

Year-class	P	Variance	σ
1.....	.79	.0267	.163
2.....	1.04	.1548	.393
3.....	.42	.0065	.081
4♂.....	.72	.0175	.132
4♀.....	.75	.0554	.235
5♂.....	.47	—	
5♀.....	.96	.1008	.317
6+♂.....	.74	.0604	.246
6+♀.....	.43	.0051	.071

LARVAL SURVIVAL

Evaluation of larval survival was not attempted on a large scale but a few data were obtained which are of significance. At Pool 2 about 5,000 eggs were deposited during late May of 1955. In September of 1955 an attempt was made to use the Lincoln index as a means of estimating numbers of tadpoles in Pool 2. Twenty-one tadpoles were marked by clipping a notch from the tail fin. Samples of 32 and 54 larvae were subsequently drawn from this pool (on September 3 and September 6) in which there were 3 and 5 marked larvae respectively. These samplings yield estimates of 224 and 227 larvae which may not be reliable for there is a possibility that the recaptures were not actually random. At Pool 3 about 7,000 eggs were laid in early June of 1955. On August 30, 1955, 79 tadpoles were marked here and in a sample of 93 taken two days later there were 12 marked larvae. These data yield a population estimate of about 600. On September 7, 1955, this pool was dry and 491 tadpoles were collected from the muddy remains of the pool. Because metamorphosis was occurring at this time the difference between 600 and 491 is due to transformation and mortality. At Pool 1 it was estimated that about 13,000 eggs were laid in late May and early June of 1955. No larvae transformed at this site before the pool dried.

CAUSES OF MORTALITY

The actual causes of mortality are difficult to work out in field studies of anurans because one rarely finds dead individuals. Even when this does occur it is usually impossible to tell why the animal died. It is probable that most of the mortality occurring in the population studied takes place during the winter hibernation. Other losses in the population, other than those due to predation, are brought about by miscellaneous factors.

Two dead frogs were found crushed by automobiles; another had apparently been stepped on. One frog was found drowned in a quiet backwater. The right hind leg of the animal was inextricably tangled in a fibrous root. Such roots are exposed beneath undercut banks which are used by frogs for protection and concealment. An emaciated male was captured with a rhyolite rock weighing 1.4 gm

stuck in the pylorus of its stomach. The weakened condition of this frog and the empty intestines indicated that the stone was not only unregurgitable but was also blocking the movement of ingested food from the stomach to the duodenum. Stones are not uncommonly ingested accidentally and apparently exceptionally large ones, which become stuck, may cause death. Ten dead frogs were found at various times during the summers of 1954 and 1955 which were probably killed by boys. An adult female frog was found with a torn flap of skin on her venter and a small gash on her chin. It is not known how the injuries occurred but six days later she was found dead. On six other occasions dead frogs were found, always in or near water, always in normal postures as though no violence occurred. In two cases there were holes or breaks in the skin but it could not be determined whether they were made before or after death. No cause of death, in any of these cases, was apparent.

Practically nothing is known concerning the natural enemies of *Rana p. pretiosa* or the amount of predation pressure to which natural populations of the western spotted frog may be subjected. The role of this frog in the food-web of the community varies over the entire range of the species so the following remarks must be interpreted as applying specifically (unless otherwise stated) to the Lake Lodge population. To begin with, attention may be focused primarily on avian and mammalian members of the community. The virtual absence of reptiles, and specifically the garter snake *Thamnophis elegans vagrans*, is of considerable significance, for garter snakes feed on spotted frogs in other parts of Yellowstone Park. Cutter (1930) found that captive garter snakes readily consumed spotted frogs.

The following mammals have been considered as possible predators.

Black bear (*Ursus americanus*).—Brodrick (1954) in writing of these bears in Yellowstone Park states that they are "omnivorous, eating anything that comes their way, grass, fruit, . . . fish, frogs etc." While this may be true under natural conditions the food habits of black bears in the vicinity of Lake Lodge have been so altered that their role in the community as carnivores is negligible.

Mink (*Mustela vison*).—During six summers only one mink was seen in the area under study but real opportunities for observations occurred only during 1953, 1954, and 1955. The mink must be recognized as a probable predator, although these animals do not seem common in the community under observation.

Coyote (*Canis latrans*).—Coyotes are common in the Lake Lodge area and their activities bring them into frequent contact with spotted frogs at times when the latter are most vulnerable to attack (in May and June when the wet meadows and shallow pools are populated). Because of the catholic tastes of the coyote the species is a possible enemy of the

frogs. Furthermore, Moore (1929) has reported the observation of a coyote apparently catching and eating tadpoles (and adults?) of *Rana boylei sierrae* (= *R. muscosa*) in the Sierra Nevada west of Bishop during July of 1928. On the other hand, neither Olaus Murie (1935) nor Adolph Murie (1940) found any evidence that the coyote utilizes *Rana p. pretiosa* as prey. Olaus Murie worked in Jackson Hole, Wyoming, and examined 64 stomach and 714 fecal samples without finding a trace of amphibian remains. Adolph Murie examined 5086 droppings from Yellowstone Park with the same results. Of course if only tadpoles were consumed one would not expect to detect their remains by an inspection of feces.

Man.—Some illegal human exploitation of spotted frogs in Yellowstone occurs, not as a source of food but rather for amusement or as fish bait.

In the case of birds there are more potential predators and the determination of what species are present regularly or commonly in the community is more difficult. Furthermore, rather unlikely species may emerge as predators. In other parts of Yellowstone Park sandhill cranes and great blue herons probably function as important predators. I have observed cranes feeding in Hayden Valley along the Yellowstone River in areas where young frogs might be expected to abound, but even with field glasses it was not possible to identify the items consumed. White pelicans have been observed capturing tiger salamander larvae (and adults?) in some lagoons and smaller lakes, but whether this proclivity may be expanded to include frogs I do not know. Actually these uncertainties need not be weighed in evaluating predation pressure on the Lake Lodge population because these birds do not occur in this particular community.

The following species are the most likely avian predators of adult frogs: Swainson hawk, marsh hawk, California gull, horned owl, great gray owl.

California gulls occasionally use the lakeshore where Soldier Creek runs into Yellowstone Lake but were not encountered in the upper (mostly wooded) part of the study area. Both owls are present but I do not believe either species is numerous. Of the two hawks which were identified, the marsh hawk was by far the more common. This hawk is the only predator operating on a scale sufficient to affect the adult population appreciably. The evidence for this assumption is indirect; no marsh hawk was ever observed to capture a frog. However, Anderson (1934) has reported that in 1929 marsh hawks were common on the Kootenay Flats in British Columbia and that both adult and young hawks were observed frequently gorging on small western spotted frogs during that summer. Furthermore, on three occasions in 1955, frogs were found with puncture wounds (or recent sears) which suggested the work of talons.

The virtual absence of the wandering garter snake (*Thamnophis elegans vagrans*) in the com-

munity has already been mentioned, and there is no established population of these snakes occupying the study area. However, on two occasions garter snakes were noted. On July 19, 1955, a juvenile was captured near the cabins along the eastern side of the area. And on July 22, 1956, an adult was observed at Pool 3. On this latter occasion I caught the snake and by palpation forced the disgorgement of a partly digested adult male frog which had been a marked member of the population.

Instances of birds preying on anuran tadpoles have been reported by Collinge (1939) and Karlstrom (1954). I first observed such activity on June 24, 1953, when a robin alighted at the edge of a puddle and began seizing and consuming tadpoles of *Rana pretiosa* from the shallow water. At this time the pool was about 14 inches in diameter with a maximum depth of about 6 inches. On July 10, 1954, at the same locality, robins were again noted feeding at the edges of the pool. On August 30, 1955, at Pool 3, two gray jays (*Perisoreus canadensis*) were observed to alight at the edge. One waded into the water a few inches, lunged suddenly and pulled out a tadpole of *Rana pretiosa*. On September 1 and 2, 1955, similar incidents involving these jays were observed at the same locality.

Another predator on *Rana pretiosa* is the larva of the dytiscid beetle *Dytiscus dauricus*. These beetle larvae develop in the same ponds as frog tadpoles and may attain lengths of as much as 45 mm. On June 22, 1954, one of these larvae was observed grasping the head of a frog tadpole, and on June 13, 1955, at the same locality, a dytiscid larva was seen with a *Rana* tadpole in its jaws.

Evidently the Lake Lodge population of *Rana p. pretiosa* is free from extreme predation pressure primarily because of the fortuitous absence of predators rather than through any behavioral modifications on the part of the frogs. Besides man, the mink is the only likely mammalian predator. Of the birds, hawks (and especially the marsh hawk) are the only likely enemies of importance. Other possible predators, although present in Yellowstone Park, are not members of the community involved. The absence of garter snakes from the area affords relief from a major predator in other parts of Yellowstone.

The larvae of the western spotted frog may be exploited to a mild degree by dytiscid larvae and to a greater extent by various passerine birds. Neither type of predation can be considered to markedly affect larval survival. The conditions appropriate for larval predation by birds almost invariably are the precursors of tremendous (or even complete) mortality of larval populations. Karlstrom (1954) states that when he observed robins eating toad larvae the water was "barely deep enough to cover their [the tadpoles'] backs." In Yellowstone the same sort of conditions existed in all instances (at Pool 1 in 1953 and 1954 and at Pool 3 in 1955) where avian predation occurred and the mortality of larvae was

nearly 100% because of desiccation. In general, only if transformation of the majority of the larval population happened to coincide exactly with an extreme reduction of the available water could consumption of larvae by birds affect population levels.

In view of what little is known of other anuran populations the Lake Lodge population of *Rana p. pretiosa* seems remarkable in at least two respects.

1. The post-metamorphic survival rate does not vary drastically between the year-classes. This differs from the condition described by Bannikov (1950) in a population of *Bombina bombina* near Moscow. Here about 98% of the first year-class perishes during the first hibernation. As a result, the population is made up of about 97% first-year individuals, 2% second-year individuals, and 1% older toads.

Jameson (1955, 1956a, 1956b) has attempted to work out survival rates in *Syrrhopus marnockii*, *Hyla regilla*, and certain other anurans by marking several hundred individuals and then returning to the same site at a subsequent date and attempting to determine the number of marked animals present. He has then compared the number of recaptured marked individuals with the original number of marked frogs and attributed the difference to "losses," whether due to emigration or mortality. Such a procedure does not furnish reliable data on survival. What Jameson has actually calculated is *minimal survival*, which constitutes but a fraction of the actual survival—this fraction varying as a function of the recapture efficiency. Blair's (1953) data on juvenal survival in *Bufo valliceps* were obtained in a similar manner but in this case the "survival" was represented correctly as *minimal survival*.

One assumption implied by my analysis of survival is that frogs of various ages are recaptured with the same efficiency. The evidence in support of this assumption is negative, i.e. there is nothing which suggests an obvious inability to recapture frogs of a certain age. However, Martof (1956b) found that green frogs of different ages were recaptured with variable success and that the smallest frogs had the lowest rate of recovery. Because the greater dispersal of juveniles contributed to this effect, the extent (if any) to which a greater juvenal mortality is indicated is not known.

2. The age composition of the Lake Lodge population is notable because of the large number of frogs 6 years of age or older, which is a reflection of the unusually long life-span of these frogs. On the whole, our conceptions of the maximal life-span of anurans have been based on records of survival in captivity. Flower (1925, 1936) and Bourlière (1946) have summarized data pertaining to the life-span of a number of species of the genus *Rana*, and Flower concluded that the normal length of life in the Ranidae is about 8 years while Bourlière suggests a *longévité moyenne* of even less. However, Cowan (1941) has reported that *Rana aurora* (a species closely related to *Rana pretiosa*) may live as long as 15 years in

captivity. Probably different populations of the same species exhibit different life-spans, the evolution of which has been governed by the particular physical and biotic conditions peculiar to the community of which the population is a part.

One may wonder what sort of environmental conditions might promote, and at the same time permit, the situation apparently existing in the Lake Lodge population of *Rana pretiosa*. First, it is likely that the relatively small annual growth increments and the protraction of the pre-reproductive portion of the life-span are related to the short growing season and the comparatively low summer temperatures. Probably also associated with the summer temperatures (because of a longer time required to produce an egg complement?) is the limited reproductive effort, which produced on the order of only 25,000 eggs in 1955. Because the population inhabits, at least in part, a marginal habitat, larval survival is poor and indeed almost nil in some years. These conditions demand a high rate of post-metamorphic survival. The long life-span of the Lake Lodge frogs is permitted by a virtual absence of predation pressure. Also the frogs must have a capacity to survive a relatively large number of hibernations. If these frogs are physiologically adapted to a slower metabolic pace, their whole life-span might correspond physiologically, though not chronologically, with the shorter life-spans which have been ordinarily associated with anurans.

One unanswered question pertains to the apparent preponderance of older females in the population. If there are no demonstrable differences in the mortality rates of older males and females and the sex-ratio is 1:1 through the fifth year of post-metamorphic life, there is no convenient explanation for the observed sex-ratio among older frogs. If older males were present, but not as susceptible to capture and recapture, this would be reflected in an apparently low rate of survival. Actually, older males were recaptured with such frequency that their calculated survival considerably exceeds that of females of the same age (Table 6). One possible explanation for the apparently low survival of old females may be that considerable effort, both in marking new frogs and recapturing previously marked ones, was expended at breeding sites (e.g. Pool 1 and Pool 3). Males breed more frequently than females, the latter breeding every other year, possibly every 3rd year. Hence, in a 3-yr study, females might be somewhat less susceptible to repeated captures than males of comparable age. Although sampling was continued throughout every summer, over the whole area occupied by the population, it was easier to collect large numbers of adults in the breeding ponds than elsewhere.

The inconsistency between the numbers of older males and their calculated rate of survival cannot, at present, be reconciled. None of the fifth-yr males marked in 1953 was recaptured in 1955 (Table 5).

This depresses the value of P somewhat but not to a significant degree. However, if pure conjecture may be permitted, one could account for the observed structure of the population by postulating a reduced survival of 5-year old males. In other words, males would survive at the same rate as females through five years of age—virtually all of the breeding males being 4 or 5 years of age (this last, at least, is true). Then, possibly as a physiological consequence of two seasons of breeding activity, and in accordance with Rubner's hypothesis there would be an increased mortality in 5-year old males, so that the older male age groups would be small.

Spatial Relationships

Movements constitute an intriguing aspect of the ecology of anurans but one which has been studied intensively in only a few forms, e.g. *Bufo t. terrestris* (Bogert 1947), *Rana esculenta* (Juszczyk 1951), *Rana clamitans* (Martof 1953), *Bufo bufo* (Moore 1954), *Scaphiopus h. holbrookii* (Pearson 1955) and *Gastrophryne olivacea* (Fitch 1956). Such studies have depended on recaptures of marked individuals and some method of recording the successive wanderings (if any) of the marked animals on maps. For the purpose of analysis movements have been assumed to be along straight lines between two points of capture. In my study of *Rana p. pretiosa* in Yellowstone Park a similar program was followed. In the course of the investigation 1663 frogs were marked. A total of 902 frogs was recaptured, about 54.2% of the total number marked. One frog was recaptured 19 times and the remainder from only once to 15 times.

Dispersion of the Population

In the study of the movements of the individuals of any one population it is important to attempt to discern at the outset any major trends in movements (whether in magnitude or direction), or basic patterns of dispersion expressed by the population as a unit. The behavior of individuals is susceptible to a more meaningful analysis following such an approach.

With this in mind, I plotted all points of capture and recapture for a series of 1144 frogs during three periods of the summer: May 21 to June 20, June 21 to July 31, and August 1 to September 20. Data from all years were lumped and every capture or recapture involving a new locality or a new time period was represented. Hence, if a frog were captured three times in the same spot on May 30, June 19 and July 3, only two captures would be recorded. This is because both May 30 and June 19 lie within the limits of the May 21 to June 20 interval. The results of this procedure are illustrated in Fig. 7. A large portion of the population apparently migrates to Soldier Creek and other permanent water during the latter part of the summer. The entire study area was not subjected to sampling of equal intensity during each of the three time periods because par-

ticular effort was made to investigate the activities of frogs in areas where they were known to occur. Nevertheless, no part of the area was ignored and although more intensive sampling of Soldier Creek during May and June would have revealed more frogs along its course, the dispersion patterns in Fig. 7 are representative. The mass movements are a response to the evaporation of water which accumulates in the meadows and transitory pools during May and early June. The rate of evaporation is in turn af-

fected by a series of factors such as precipitation, exposure, humidity, wind, etc., of which the first is probably most important (see under Physiography and Vegetation). Where there is permanent water or where there are pools which persist into late summer (e.g. Pools 2, 3, and 4) there are no major shifts.

An obvious question arising from this analysis of the whole population concerns the influences of age and sex, if any, on the dispersion patterns. From what had been learned of the growth rates in the population it was possible to assign the majority of captured frogs to appropriate age-groups. When there was doubt as to the age of a frog it was excluded from consideration. Frogs presumed older than 5 yrs were treated as a group. Sexes were treated separately for the 4th, 5th and later years. Patterns of dispersion were then prepared for the first 5 yr-classes and for older males and females. This procedure revealed differences associated with age and sex which may be summarized as follows:

1st, 2nd and 3rd year-classes.—These young frogs all tend to occupy upland habitats during May and early June but first-yr frogs do not inhabit larger ponds (e.g. Pools 1, 3, 4) of the type that may be used for breeding. Just why these smallest frogs are restricted to the flooded meadows or shallow intermittent stream courses at this time is not known. An appreciable percentage of the 2nd and 3rd yr-classes may occupy the larger pools and after the cessation of breeding activities 2- and 3-yr old frogs may be fairly numerous at Pools 1 and 3 (Fig. 8A). During August, Pool 3 and 4 may still be occupied by younger frogs but the bulk of the first three yr-classes is scattered along Soldier Creek and concentrated around Pool 2 or in adjacent marshy areas.

4th and 5th year-classes.—In the 4th yr after transformation males breed for the first time, and while the upland habitats are again invaded during May and early June it is now the potential breeding sites which are occupied (Fig. 8B). However, the distribution of 4th yr females at this time resembles that of the first three yr-classes. The similarity of the behavior of the 4th-yr females and younger frogs is heightened by their similar utilization of Pool 1 after breeding activity is over (Fig. 8C). I can discern no difference between the behavior of 4th- and 5th-yr frogs—one finds the males congregated around Pool 1 and Pool 3 during May and early June, the females deferring their occupation of such sites until late June.

Older males.—Older males were found most commonly at Pool 1 and Pool 3 in May and early June. Their behavior during the remainder of the summer apparently conforms to the usual pattern.

Older females.—The dispersion of older females during May and early June suggests that this group (whatever its age limits) constitutes the majority of the breeding females in the population (Fig. 8D). During late June and early July these frogs remain at the pools until they are forced to return to Soldier Creek.

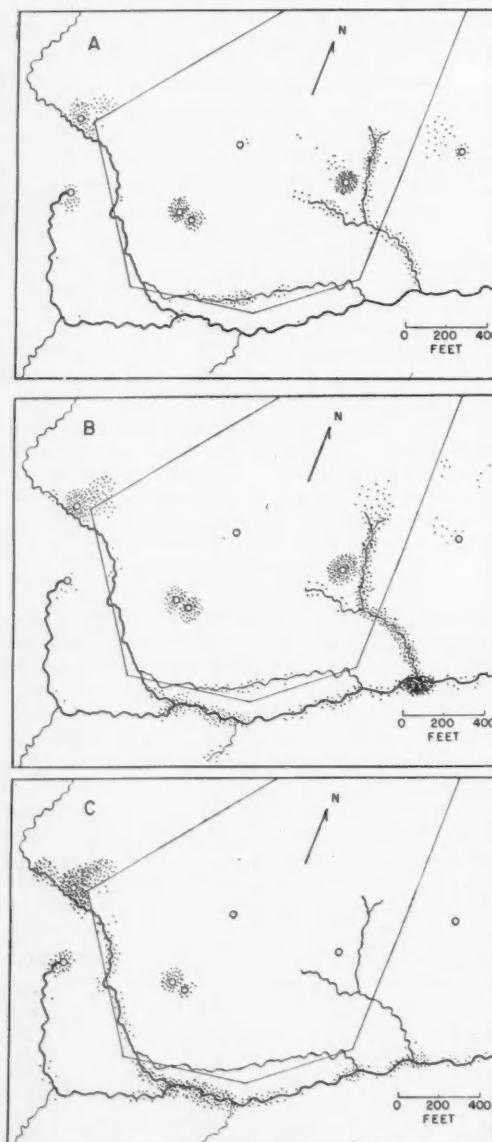


FIG. 7. Dispersion of the Lake Lodge population of *Rana p. pretiosa* during (A) May 21 to June 20, (B) June 21 to July 31, and (C) August 1 to September 20.

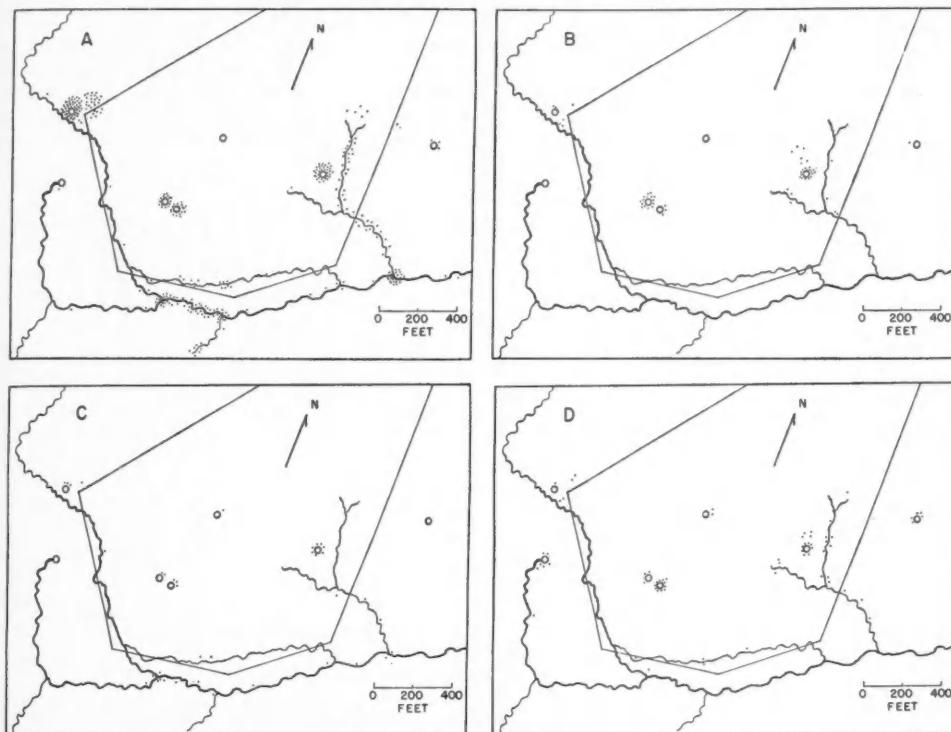


FIG. 8. Dispersion of *Rana p. pretiosa* of the Lake Lodge population. (A) 2- and 3-yr old frogs between June 21 and July 31, (B) 4-yr old males between May 21 and June 21, (C) 4-yr old females between June 21 and July 31, and (D) older females between May 21 and June 20.

Mass migrations of frogs from winter hibernacula to breeding sites apparently occur regularly in a number of species of anurans. Even as early as 1887 Ballou described mass movements of frogs (*Rana pipiens*?) from hibernation sites at the bottom of a river to prairie sloughs where they bred and remained until the fall, at which time they returned to the river. Juszczyk (1951) observed that in *Rana esculenta* there are two distinct periods of migration, one in the spring when the frogs move away from streams and another at the end of the summer when they return. Comparable behavior has been demonstrated in other anurans. In my study it is clear that there are two periods of maximal movements each summer, one in May and the other in July. However, the return to Soldier Creek is governed by the drying of the meadows and transient pools and the peak of activity occurring in July primarily reflects returns to Soldier Creek from Pool 1 and the meadows in the eastern part of the study area. Frogs remain at Pool 3 and Pool 4 (in progressively decreasing numbers) until these pools dry in late August or September.

These major movements are carried out by all members of the population, and no significant differences in distances moved or rates of movement

were found associated with sex or age differences. Fiteh (1956) states that male *Gastrophryne olivacea* move farther than females, and Anderson (1954) concluded that a similar condition exists in *G. carolinensis*. Pearson (1955) found no sex differences in movements of *Scaphiopus holbrookii* but concluded that the smallest toads moved farthest. He also showed that differences in population density and habitat were related to differences in distances moved. Possible differences owing to changes in population density were not investigated in my study, but it is true that the nature of the habitat, as well as the location of certain physiographic features (e.g. ponds) in it, influences the patterns and hence the magnitude of movements in the population. On the other hand, Juszczyk (1951) found that *Rana esculenta* dispersed in all directions from the streams and that the direction of movements was not at all related to topography.

RATE OF MOVEMENT

The seasonal changes in the dispersion of the population suggested that there might be seasonal variation in the rate of movement; therefore, the following analysis was made.

TABLE 7. Seasonal changes in rate of movement by *Rana p. pretiosa* in the Lake Lodge population. All age groups and sexes combined.

	May 21-June 10	June 1-June 20	June 11-June 30	June 21-July 10	July 1-July 20	July 11-July 31	July 21-August 10	August 1-August 20	August 11-August 31	August 21-Sept. 10	Sept. 1-Sept. 20
Number of movements treated....	107	54	139	52	204	38	69	15	31	13	21
Range (feet/day)...	0-350	0-125	0-150	0-79	0-620	0-133	0-205	0-33	0-142	0	0-15
Mean (feet/day)...	8	10	13	20	48	12	7	8	8	0	2

The four-month period between May 21 and September 20 was divided into 11 overlapping 20-day periods (i.e. May 21-June 10, June 1-June 20, June 11-June 30, June 21-July 11, etc.) and all movements taking place within the limits of any of the eleven 20-day periods were appropriately grouped. Movements taking place over a period of time longer than 20 days were excluded, but the samples were considered adequate. Movements were calculated to the nearest 10 ft, and the feet moved per day calculated from this value and the days elapsed between the successive captures. Some of the assumptions inherent in this method may not be valid, but no other index of rate of movement is available. The results of this procedure are presented in Table 7. The major movements involved in the return of the population to Soldier Creek occur during late June and the first three weeks of July, and movements during the remainder of the summer are less extensive.

Here again the possible influence of age or sex on rate of movements was investigated by examining the movements of the same age-groups of frogs which were treated in the study of dispersion. This analysis revealed that all year-classes and both sexes conform to the general pattern indicated in Table 7—in fact the similarity between the first three year-classes was quite striking. An inspection of the rate of movements of adult males and females (4 yrs or older) showed that between May 21 and July 21 the average rates were, as a rule, higher for females, but none of these differences was significant.

Some idea of the maximum rate at which spotted frogs may travel may be gained by examining the records indicating the fastest movement. It can only be hoped that a fairly accurate indication of the maximal rate has been obtained by chance. Table 8 summarizes the 15 most rapid movements revealed in this study. *Bufo bufo* has attained rates of 350 m in 2 days (570 ft per day) according to Herter (1941). An immature *Rana catesbeiana* moved 3000 ft in 4 days (Raney, 1940) and McAtee's (1921) 3-footed bullfrog moved about 1300 ft in 2 days. Breder *et al.* (1927) found that male Fowler's toads would travel at least 0.25 mile in less than 24 hrs when returning to their "home" pond. Actually, it is likely

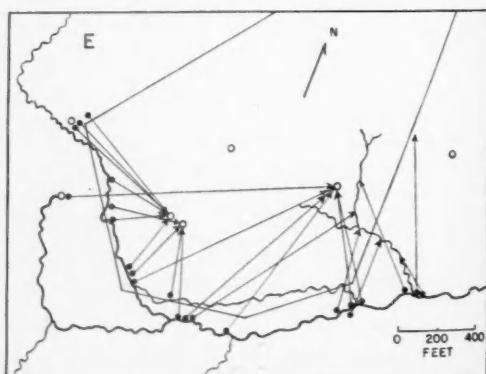
TABLE 8. Maximal rates of movement of *Rana p. pretiosa* in the Lake Lodge population. Plus mark in age column denotes an age greater than 5 years.

Sex	Age	Feet moved	Days elapsed	Feet/day (nearest 5)
♀	+	620	1	620
	2	480	1	480
♀	+	330	1	330
♀	+	300	1	300
♂	4	300	1	300
♂	+	1030	4	255
♀	+	500	2	250
♀	+	470	2	235
♂	+	450	2	225
♀	+	410	2	205

that none of these rates are accurate indices of the animals' maximal capacities. Moore (1954) followed migrating toads (*Bufo bufo*) and reported that, on the average, toads moved about 100 yds per hr but that one female moved 204 yds in 1 hr. Moore estimated that normally toads probably take about 24 hrs to move 0.75 mile.

MOVEMENTS FOLLOWING EMERGENCE

There is an important inference which is suggested by Table 7 and Fig. 7. The rate of movement during late May and the first half of June seems in-

FIG. 9. Movements of 22 *Rana p. pretiosa* of the Lake Lodge population following emergence in May.

adequate to account for the invasion of the upland habitats from the hibernacula along Soldier Creek and around its source. It seems likely that a spate of movements must occur prior to May 21, and that investigations were not commenced early enough to

reveal it. Some appreciation of the magnitude, if not the rate, of these movements which follow emergence may be gained by comparing the location of frogs when last captured in September of one year and when first recaptured in May or early June of

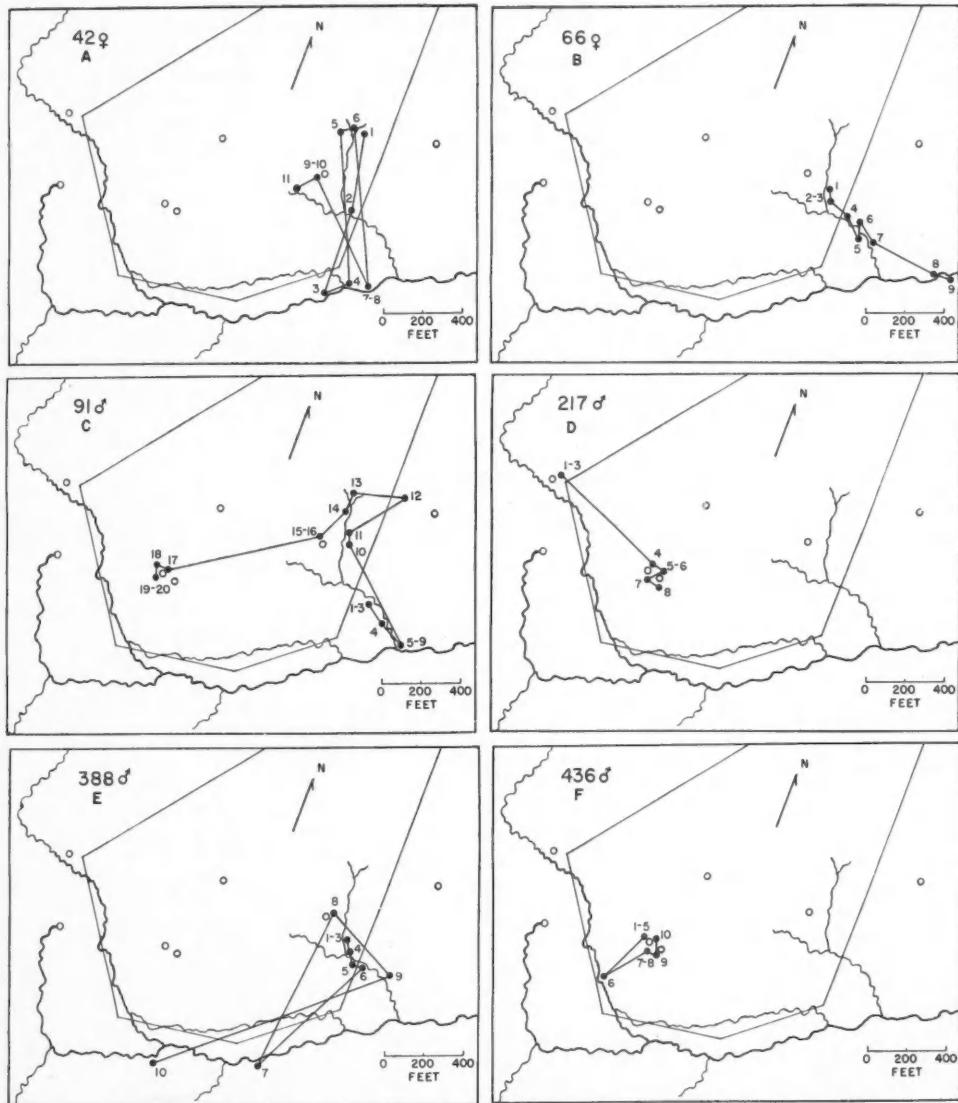


FIG. 10. Movements of 6 individual *Rana p. pretiosa* of the Lake Lodge population. Capture dates as follows: Individual No. 42—1, 6/22/53; 2, 7/2/53; 3, 7/15/53; 4, 7/28/53; 5, 6/22/54; 6, 6/26/54; 7, 9/9/54; 8, 9/13/54; 9, 5/24/55; 10, 5/28/55; 11, 6/13/55. Individual No. 66—1, 6/28/53; 2, 7/1/53; 3, 7/3/53; 4, 7/4/53; 5, 7/5/53; 6, 7/6/53; 7, 7/15/53; 8, 7/28/53; 9, 8/4/53. Individual No. 91—1, 7/1/53; 2, 7/2/53; 3, 7/4/53; 4, 7/5/53; 5, 7/19/53; 6, 7/22/53; 7, 7/28/53; 8, 8/4/53; 9, 8/14/53; 10, 5/31/54; 11, 6/12/54; 12, 6/18/54; 13, 6/26/54; 14, 6/29/54; 15, 6/20/55; 16, 6/26/55; 17, 8/3/55; 18, 8/25/55; 19, 8/30/55; 20, 7/24/56. Individual No. 217—1, 8/18/53; 2, 9/3/53; 3, 9/6/53; 4, 6/4/54; 5, 7/5/54; 6, 5/28/55; 7, 6/6/55; 8, 7/3/55. Individual No. 388—1, 5/29/54; 2, 6/3/54; 3, 6/8/54; 4, 6/12/54; 5, 7/1/54; 6, 7/4/54; 7, 8/8/54; 8, 5/27/55; 9, 6/7/55; 10, 8/8/55. Individual No. 436—1, 6/3/54; 2, 6/12/54; 3, 6/18/54; 4, 6/30/54; 5, 7/5/54; 6, 9/1/54; 7, 5/21/55; 8, 6/6/55; 9, 7/3/55; 10, 7/24/56.

the next year. There is not much movement during September so it is likely that any differences in these locations has been brought about by movement following the spring emergence. Such movements for 22 frogs are plotted in Fig. 9.

PATTERNS OF MOVEMENT

Because some features of the study area served as focal points of activity or governed the patterns of movements, an analysis of the role of certain ponds and stream courses was made in an effort to determine whether particular routes were more or less invariably utilized. The following conclusions reflect behavioral modes and the reader is referred to Figs. 10 and 11 for records of movements of individual frogs which support these conclusions.

Pool 2.—Pool 2 is used as a place of hibernation and in some (but not all) seasons as a site for egg deposition. Most of the dispersal from this pool is into the immediately adjacent marshy areas (Fig. 11A). From these areas further dispersal occurs to other parts of the area. Some members of the breeding congresses in Pool 3 come from Pool 2 (Fig. 10D).

Pool 3.—Pool 3 is regularly used as site of oviposition. Its occupants during May and June come almost without exception from the western portion of Soldier Creek (Fig. 10F) and from Pool 2 and its

environs. Later in the summer frogs may move to Pool 3 from Pool 1 and the marshy areas in the western portion of the study area as these latter features dry out (Fig. 10C). Dispersal from Pool 3 is of two general types: 1) directly back to Soldier Creek and the vicinity of Pool 2 or 2) to Pool 4 (Fig. 10F). Movements to Pool 4 usually presage an ultimate return to the southwestern portion of Soldier Creek, or a movement to Pool 1 or elsewhere in the eastern part of the study area (Fig. 11B).

Pool 4.—Although Pool 4 is not used for breeding, it is occupied by frogs from the time it forms in May until its evaporation in August. Its population is drawn from the Pool 2 area and the southern and western part of the study area. These points are illustrated in Fig. 11C. Dispersal from Pool 4 is usually to the southern part of Soldier Creek and to a lesser degree to Pool 3 and the eastern part of the area.

Pool 1.—Frogs congregate at Pool 1 primarily from the eastern portion of Soldier Creek and the meadows in the eastern part of the study area (Fig. 10A, C). There is, however, appreciable movement to Pool 1 from Pools 3 and 4, and even the southwestern part of Soldier Creek (Fig. 10D). A few frogs come to Pool 1 from the Spring 1 area. These points are illustrated in Fig. 11D. Dispersal is to the same places from which the frogs come.

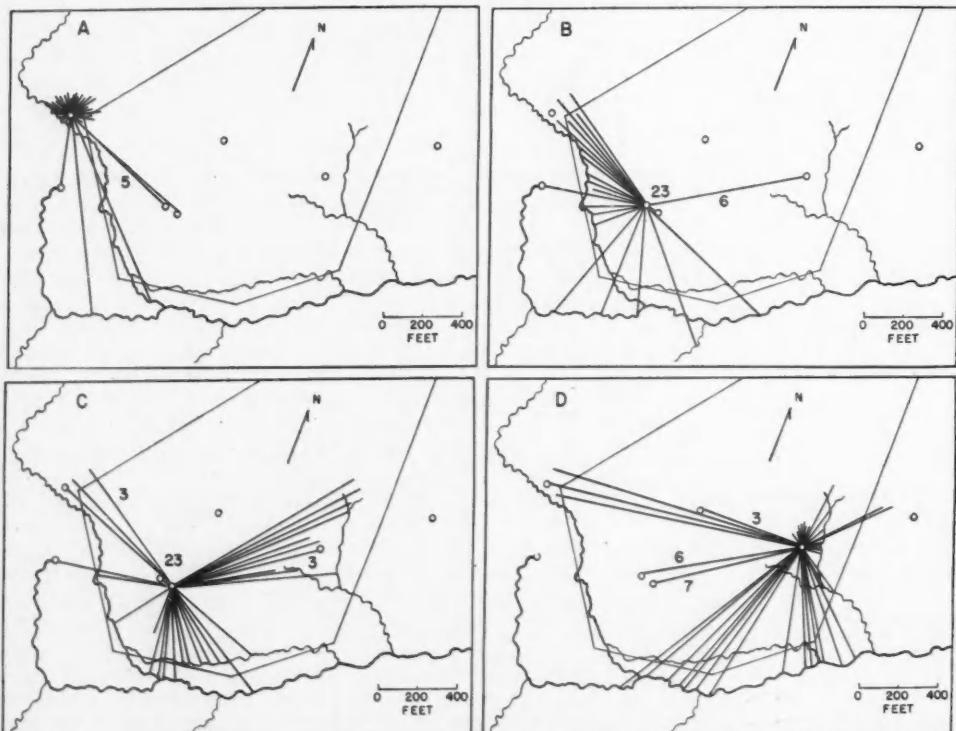


FIG. 11. Patterns of movement of *Rana p. pretiosa* in the Lake Lodge population involving (A) dispersal from Pool 2, (B) dispersal from Pool 3, (C) movements to Pool 4, (D) movements to Pool 1.

Other.—During late May and early June, a boggy area on the eastern side of the study area is rather heavily utilized by frogs. This area is invaded in the spring by frogs moving north from the southeastern portion of Soldier Creek, though it is possible that frogs move into it from the north too. The immediate dispersal of frogs, as the area dries, is towards the intermittent stream course and back to Soldier Creek (Fig. 10C), but ultimately frogs from this area may reach the western portions of Soldier Creek. The westernmost branch of Soldier Creek, originating in part at Spring 2, is invaded by frogs primarily from the Spring 1 area and Pool 3.

The data relating to dispersal of frogs from and to various features in the area illustrate that exchanges between the westernmost portions of the Soldier Creek drainage and the meadows around Pool 1 regularly occur. These movements involve distances of 1200-1500 ft and may take place in one season or over a period of several seasons. Movements along Soldier Creek are primarily upstream. Because the Spring 1 area (and specifically Pool 2) at the source of Soldier Creek represents the only breeding site where reproductive effort is assured of some degree of success, it would seem advantageous for movements along Soldier Creek to be upstream. Such movements would draw the population towards Spring 1 and perhaps insure a breeding population of greater size in the area where success is greatest. Martof (1953) reported that in *Rana clamitans* upstream movements were exhibited by 72% of the newly transformed frogs and about 60% of the adults. However, in this case upstream was *away* from the breeding area, so apparently not all the factors inducing upstream movements are understood.

The routes involved in these movements, although treated as straight lines, are of course not of such a nature. Some evidence very clearly shows that returns to Soldier Creek from the eastern part of the area are by way of the intermittent stream course (Fig. 10B), and it is probably appropriate to visualize the majority of movements taking place in the latter part of the summer as being restricted to streams or intermittent water courses which still retain water. Naturally, however, movements to Pools 1, 3 and 4 in the spring necessitate overland movements, and there probably is an appreciable amount of cross-country travel in May and June, most of it occurring at night. The evidence for this last assumption is indirect, and is based on the fact that frogs were found moving overland during the day on only about half-a-dozen occasions during the entire study. Direct overland movements are also involved in movements between Pool 1 and Pools 3 and 4 and vice-versa, and between Spring 1 and 2, as frogs were captured occasionally between these points. In fact, although *Rana pretiosa* has been repeatedly described as a "highly aquatic" frog—one restricted to water and rarely moving far from the banks of permanent streams—spotted frogs *will* utilize upland

situations for long periods of time if there are scattered puddles and sufficient cover available.

EMIGRATION

If one considers emigration as irreversible movements of individuals resulting in the reduction of the size of a population, one must define the geographical limits of the population in question before one may determine which movements constitute emigration. In this study it was found that Soldier Creek and its drainage seemed to support a spatially well-defined population of frogs. The lower portion of Soldier Creek was excluded from intensive study, and because of the fact that there are no regularly successful breeding sites between the western portion of the drainage and the point at which Soldier Creek runs into Yellowstone Lake, this exclusion is not as artificial as it may seem. For this reason, movements of frogs from the western portion of the drainage (nearer the source of Soldier Creek) to the southeastern portions of Soldier Creek (at its mouth) have been considered emigration, although in the strictest sense these movements are within the limits of the population. These movements could theoretically be reversible but they probably effect a lasting reduction in the number of frogs occupying the area which was most intensively studied. These losses are probably balanced by immigrations of frogs from the southeastern portion of the Soldier Creek drainage. Fig. 12 illustrates the cases of emigration from the population studied. Because of unequal sampling effort in various areas adjacent to the study area, no conclusions as to the relative frequency of emigration to other regions may be drawn. Hotel Creek is a spring-fed stream which runs past Lake Hotel and into Yellowstone Lake about 1.6 mi south of Lake Junction. What I have termed Surprise Creek is an apparently heretofore nameless creek originating from springs about 100 yds west of the highway approximately 300 yds south of Lake Junction. It runs into Yellowstone Lake very near to the outlet of the Yellowstone River.

Most of what has been considered emigration involves movements down Soldier Creek, but movements from the Soldier Creek drainage into the adjacent drainages of Hotel Creek and Surprise Creek also occurred. The movements from the western to the southeastern part of Soldier Creek probably all occurred along the stream course but, as has been pointed out, frogs are not restricted to water courses in their travels. One male, in the course of a year (June 26, 1954, to June 23, 1955), moved at least 1300 ft to a transient pool existing in an area well isolated from any stream. In view of the ephemeral nature of this pool, it must be assumed that the movements occurred during the early part of the summer of 1955. From what point the overland trek was initiated is not known, but it was certainly not the point at which the frog was captured in 1954. (Fig. 12, No. 76). Furthermore, one needs but to examine

the movements of frogs 254, 746, 1250, 1295, 1297, and 1549 (Fig. 12) to see that overland movements of some magnitude occur. However, the series of marked frogs recaptured along Surprise Creek suggests how frogs may shift from one drainage to

another without actually moving great distances overland. The intermittent portions of Surprise Creek and one branch of Soldier Creek drain opposite sides of the same ridge. During the early part of the summer it would be possible for a frog to cross this

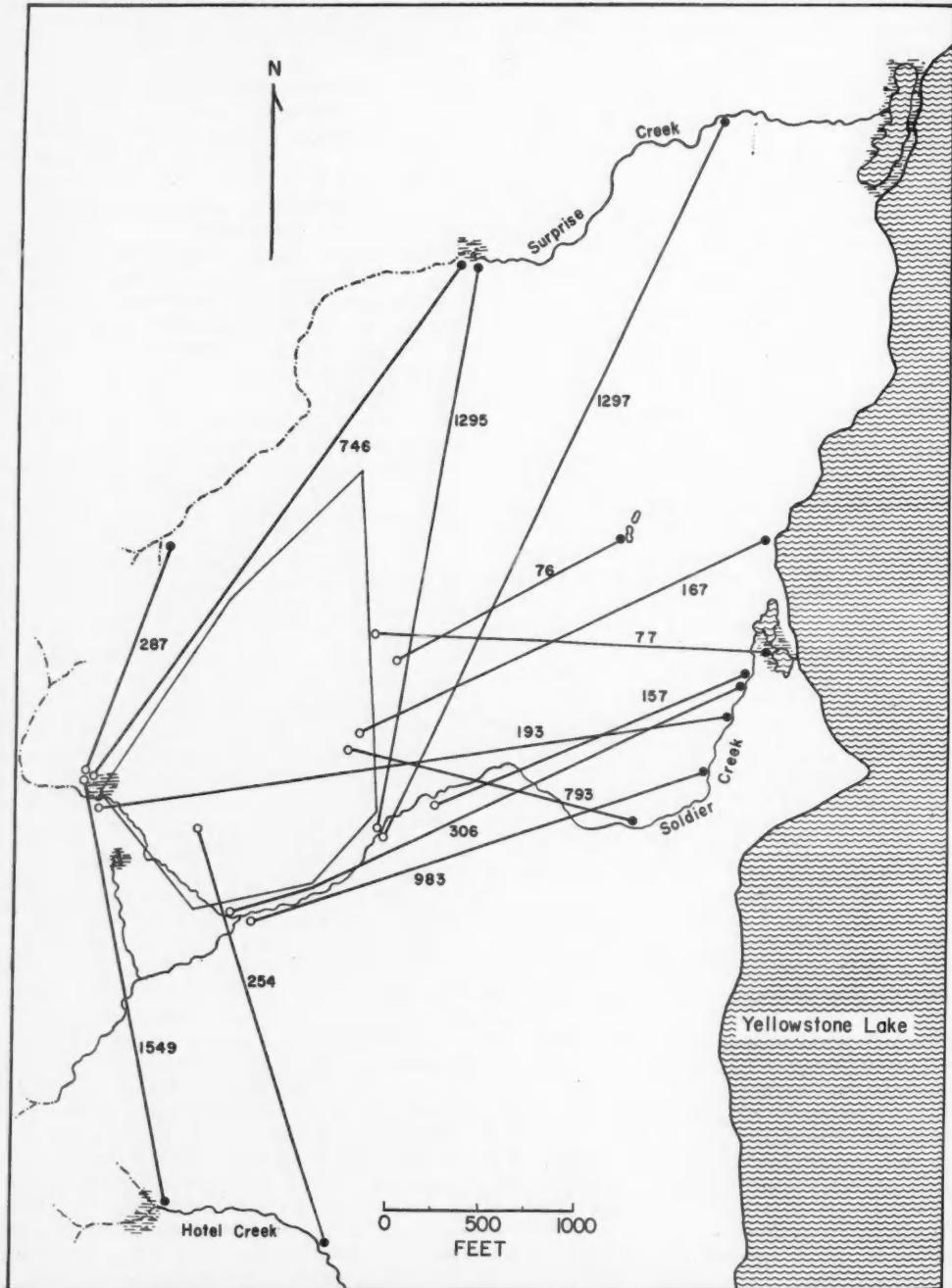


FIG. 12. Emigration by *Rana p. pretiosa* from the Lake Lodge population.

ridge from one drainage to the other with an overland journey of little more than 500 ft. It seems likely that such transfers were made by frogs 287 and 746 and probably by 1295 and 1297. On the other hand, movements into this drainage probably occur directly from the northern part of the meadow in the corral. On July 10, 1955, a group of 13 frogs was found in the northern part of the meadow. All these frogs were hopping north in what seemed to be an exodus from the drying meadow. None was ever recaptured; possibly some or all of them reached the upper part of the Surprise Creek drainage. Movements of the same kinds as hypothesized above would enable shifts to Hotel Creek from Soldier Creek. Frog 1549 was able to effect this last movement in only 23 days. This move involved a straight-line distance of about 2300 ft, whereas had this frog followed stream courses where possible the distance would have been on the order of 3500-4000 ft. The roundabout route cannot be rejected on the ground that not enough time was available.

The maximum movement occurring between two successive captures was that of frog 1297 which moved at least 4200 ft between September 16, 1954, and August 5, 1955. Other emigrations, ranging from 1250 to 3400 ft, were also recorded. If the period of the summer during which movement may occur is arbitrarily set as May 10 to September 20 then the total available days involved in these emigrations may be calculated. These results are summarized in Table 9.

TABLE 9. Emigration by 13 *Rana p. pretiosa* from the Lake Lodge population.

Frog	Sex	Dates	Number of days available for movement	Feet moved (nearest 50 feet)
287	♀	6-29-54 to 7- 3-55	144	1250
76	♂	6-26-54 to 6-23-55	131	1300
793	♀	7-10-54 to 7- 4-55	128	1600
137	♂	8- 7-53 to 8- 8-55	269	1700
77	♀	6-29-54 to 6-20-55	97	2000
254	♀	7- 5-54 to 8- 9-55	168	2300
167	♀	6-29-54 to 8- 8-55	146	2400
983	♀	9-17-54 to 7- 4-55	59	2500
306	♀	9-11-53 to 8- 8-55	234	2900
1295	♀	9-13-54 to 8- 5-55	95	3000
746	♂	8- 1-54 to 8- 5-55	138	3300
193	♀	8- 7-53 to 8- 8-55	269	3400
1297	♀	9-16-54 to 8- 5-55	92	4200

Ingram & Raney (1943) reported a movement of 5250 ft by a bullfrog and Willis *et al.* (1956) recorded movements of 0.75 mi by the same species. Bogert (1947) recorded homing movements by *Bufo t. terrestris* up to a mile; A. P. Blair (1943) reported moves of 1800 ft by *Bufo americanus* and 1100 ft by *B. fowleri*. Fitch (1956) found that whereas movements of over 400 ft by *Gastrophryne olivacea* were unusual, shifts as much as 2000 ft occurred. Martof (1953) records migrations of about 1000 ft by *Rana clamitans*. Moore (1954) reports

the recovery of a toad 2.25 mi from the point marked, and observes that this probably approaches the maximum distance travelled during breeding migrations. Except for the data of Moore, our conceptions as to how far anurans may move are restricted more by the scope of our investigations than by the capacities of the animals themselves. It was not possible to evaluate the quantitative impact of emigrations on the population of *Rana p. pretiosa* studied, but on a long range basis emigration is probably closely balanced by immigration.

HOME AND ACTIVITY RANGES

In general, the conception of the anuran home range adopted by earlier workers has been based on that of Burt (1943) and Dice (1952), who restrict the area considered as an animal's home range to that area over which an individual habitually travels while engaged in its usual daily activities. Hence, the area occupied during migrations, associated with breeding or otherwise, is not considered a part of the home range. According to this conception the home ranges of *Rana p. pretiosa* are probably on the same order of magnitude as those of other anurans which have been studied. Locations of frogs were not customarily recorded exactly enough to justify a calculation of such small areas, but in many cases frogs were captured in the same pool, or at the same spot at the edge of a pond, or in the same place along a stream, over a period of days or even several months. The longest occupations of a single spot occurred at Pool 2 or nearby, where requirements for breeding, feeding and hibernation are satisfied in one location. However, an adult female occupied the same small cove at the edge of Pool 4 between June 3 and July 5, 1954. On the eleven occasions when this frog was taken at Pool 4 it was sitting in the same spot 10 times and once was floating in the pond about 10 ft from its accustomed location. Another frog occupied the same small pool at the edge of Soldier Creek between July 7 and September 11, 1953. During this interval it was taken on 10 occasions in the same place and in fact probably hibernated there during the winter of 1953-54.

Generally, fixed home ranges exist only from late July until September, when the frogs have established themselves along Soldier Creek or near other permanent water. Of 22 frogs captured along a 900-ft section of Soldier Creek more than three times between July 6 and September 6, 1953, 10 showed no movement, 3 exhibited only slight movements (on the order of 20-30 ft), and 9 made extensive movements. The same 550-ft section of the creek was studied again in 1955 and of 6 frogs captured twice or more between July 27 and August 25, 4 remained in one spot. Furthermore, 21 frogs captured along this portion of Soldier Creek during 1954 were recaptured in 1955 and 12 of these were in their original locations.

There is a time in June and early July when shifts of location occur so frequently that it is impossible to visualize a fixed home range. Consequently, it is more meaningful to delimit the area occupied by frogs over an entire season or even a number of seasons. Such an area might be designated the "activity range" of the animal, but whatever it is called it affords a better idea of the space actually utilized by the frogs in the course of their existence. The importance of this fact became evident as it was repeatedly observed that, over a series of summers, the same frogs were found in the same general localities at the same time each year (Fig. 10C, E, F). Naturally, major changes of location were observed too, but in many cases it was found that frogs occupied the same area year after year, their cyclic migrations sometimes bringing them to the same spot they occupied exactly a year before (Fig. 10A).

By connecting the points of capture in the same way that "minimum" home ranges are delimited (Mohr 1947), an approximation of the "activity range" (incorporating migrations) can be obtained. Eighty-six of these ranges were plotted on a map of the study area and their extents determined with a planimeter. The ranges selected were, on the whole, of frogs captured 5 times or more. Where it appeared that a frog changed its location permanently during the course of the observations, and there was no evidence of return to the original area, only those points within the original range were considered. A preliminary inspection of the measured areas revealed an extreme variation in size (2500-357,000 sq ft). In order to determine whether age or sex influenced the size of the activity range, three samples of frogs which showed evidence of permanent occupancy of the southeastern part of the study area (Pool 1 and vicinity) were prepared. The ranges of 17 juveniles (1-3 yrs old), 13 males (4 yrs or older) and 28 females (4 yrs or older) were analyzed. The same 58 ranges were also analyzed for possible differences associated with the time elapsed between first and last captures of the frogs involved, because the duration of observation ranged from one month to three years. Finally, the possible influence of the geographical make-up of three different sectors within the total study area was investigated. The first of these areas was Pool 1 including the adjacent meadows, the intermittent stream course, and the eastern part of Soldier Creek. The second included Pool 3 and Pool 4, as well as the western part of Soldier Creek, and in some cases portions of the Spring 1 area. The third area was restricted to the vicinity of Pool 2 and the Spring 1 area. Activity ranges typical of these three areas are illustrated in Fig. 13. The results of these analyses are summarized in Table 10 and it may be observed that the size of the activity range is correlated significantly only with the geography of the area inhabited.

What were considered to be permanent shifts in activity range were frequently observed. The cri-

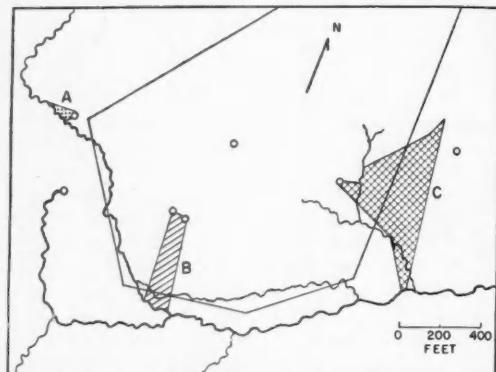


FIG. 13. Typical activity ranges of *Rana p. pretiosa* in 3 different sections of the Lake Lodge area.

TABLE 10. Analysis of extent of activity ranges of *Rana p. pretiosa* in the Lake Lodge population. Means are considered to differ significantly when there is no overlap of twice the standard errors of the means.

	Class	N	Range (sq ft)	Mean (sq ft)	Variance (nearest 1000)	Standard error of the mean (nearest 100)
Age and sex	Juveniles	17	9000-212300	65000	70000	16900
	Males	13	3000-357000	100000	96000	26800
	Females	28	3800-322000	88000	79000	14900
Sector of study area permanently occupied	Pool 1	41	3000-357000	93000	85000	13200
	Pools 3 & 4	10	4800-75500	20000	21000	6600
	Pool 2	6	2500-24400	4000	3000	1200
Time elapsed between first and last captures	less than 1 year	14	3000-230000	82000	79000	21000
	more than 1 year but less than 2 years	22	3800-357000	78000	93000	20000
	more than 2 years but less than 3 years	21	21600-223000	88000	62000	13600
	more than 3 years	1	32000	—	—	—

teria for judging such shifts were 1) the magnitude of movements (usually 1000 ft or more) and, more important, 2) the failure to return to the original area (Fig. 10C, E). Movements of as much as 900-1200 ft or more occurred in some cases but these movements did not constitute permanent shifts of activity range. Conversely movements of as little as 500 ft sometimes suggested the permanent relocation of a frog.

Quantitative data pertaining to the home ranges of *Syrrhophus marnocki* (Jameson 1955), *Scaphiopus h. holbrookii* (Pearson 1955), *Rana clamitans* (Martof 1953), and *Bufo woodhousei fowleri* (Stille 1952) indicate that anurans have small home ranges, ranging from as little as 100 sq ft in *Scaphiopus* to around 4000 sq ft in *Syrrhophus*. Small home ranges

are exhibited by *Rana p. pretiosa* during the latter part of the summer, and in certain habitats permanently. Where the ecological demands of the frog are satisfied in a relatively small area, such as the vicinity of Pool 2, home ranges may be permanently established and on the order of 2500-3000 sq ft. Other frogs carry out periodic spring migrations from Soldier Creek to upland situations, returning to the stream later in the summer. In any case, frogs tend to occupy one section of the study area, to remain there, and utilize it in the same manner year after year. Even in a study of such brief duration as that of Carpenter (1954) with *Rana pretiosa* in Jackson Hole it could be shown that "when the movements of individuals captured three or more times are plotted the resulting patterns indicate that there is a tendency for individuals to return towards the point of original capture . . .".

The best conception of the spatial requirements of *Rana p. pretiosa* is gained by considering the area occupied by a frog over one or more entire seasons, an approach similar to that advocated by Mohr (1947) for studies of mammalian activity ranges. While the variation in size of such activity ranges is great, significant differences were found associated with the geographical make-up of three different sections of the study area. Jameson (1955) concluded that the home ranges of *Syrrhophus marnocki* varied significantly with the ecology of the area, but Pearson (1955) did not find differences in *Scaphiopus holbrooki* home ranges in different habitats. No differences in size of activity ranges of *Rana pretiosa* were found associated with age or sex. Significant sex differences were not evident in *Syrrhophus* (Jameson 1955) or *Scaphiopus* (Pearson 1955). Both Jameson and Pearson point out that the number of captures, or indirectly the period of time over which an animal is observed may influence the size of the home range. Pearson (1955) found that the apparent size of the home range of *Scaphiopus holbrooki* is correlated with the number of captures, but not with the length of time the animal was studied. In my study it was found that there were no significant differences in the size of activity ranges of frogs observed from one to three months to as long as three years. In this conjunction it must be stressed that the actual number of captures is not what is important in *Rana p. pretiosa*. What is critical is the distribution in time of the captures. If the actual dates of captures in the case of those frogs observed for short periods of time (1-3 months) are examined, it develops that the short-term sample is made up exclusively of frogs, the captures of which occurred between late June and early August, or at a time when maximal movements take place. What the data really show, then, is that the extent of the activity range of a spotted frog is well indicated by its movements during one season, if the captures are distributed over the 6-8 week period when the most active movements occur. It is evident that observa-

tions of a frog for a 6-8 week period between late July and September would be likely to give a very incomplete picture of its total activity range. Major shifts of activity ranges have been demonstrated in all anurans which have been intensively studied; indeed Fitch (1956) classes such movements as one of four basic types which may be exhibited by *Gastrophryne olivacea*. *Rana p. pretiosa* may make similar movements. Just why certain frogs, both adults and juveniles, carry out these major relocations is not known. Perhaps it is a random process stimulated by subtle changes in population density or structure not yet revealed.

INFLUENCE OF PRECIPITATION AND TEMPERATURE ON THE BEHAVIOR OF FROGS

I have not found it possible to determine all of the ways in which precipitation and temperature affect the structure and dynamics of the population in question. Indeed such a task, which would ultimately involve an analysis of the entire community, is beyond the scope of this work. However, certain of the more obvious influences of these factors may be pointed out and in some cases the associated data may be developed quantitatively.

The amount of precipitation was abnormally low in 1953 and 1955; 2.73 in less than the 31-yr mean during June, July, and August of 1953, and 1.06 in less than normal for the same months in 1955. However, 1954 was wetter than usual, rainfall in June, July, and August exceeding the long-range mean by 1.29 in. It may be observed, then, that the amount of rainfall is evidently correlated with the times at which various ephemeral pools in the study area cease to exist. However, the amount of summer rainfall is not so clearly correlated with larval survival as might be expected. It may be recalled that the replacement in 1954 was estimated at about 550 individuals—yet the summer of 1953 was drier than usual. The 1955 replacement was very scant—yet the summer of 1954 was wetter than usual. This paradox may be explained, in part, by the selection of sites for oviposition. Pool 1 never contributed substantially to recruitment—regardless of summer precipitation. Pool 3 persists long enough so that some transformation always occurs among its larval population. Pool 2, the permanent spring, will invariably permit the development and transformation of some larvae if eggs are deposited there. In 1954 no eggs were laid in Pool 2, while in 1953 and 1955 oviposition took place in this spring. The behavior of adult frogs is also affected by precipitation (or lack of it) in that evaporation of the pools and the drying of the upland meadows forces a shifting of the population to permanent water. Although this point has already been brought out, the data were not treated so as to demonstrate differences in the timing of the return to Soldier Creek associated with varying amounts of early summer rainfall.

Temperature impinges either directly or indirectly on almost every facet of the ecology of the western spotted frog. In an attempt to assess the influence of water temperature on the activity of *Rana p. pretiosa*, records of captures of frogs from 10 sites within the study area (at which water temperatures were assumed to represent the best expression of the temperature conditions to which the frogs were exposed) were examined. Particular attention was given to water temperatures and times of day when these sites were sampled, and the number of minutes spent in making each census was computed to serve as an index of effort. It was thus possible to determine the relative facility of captures at different water temperatures and at different times of the day, and it has been assumed that the rate at which frogs may be captured is an index of their availability, and hence activity. Frogs which were observed but not captured were recorded as though they had been taken in the sample.

Frogs were taken in water ranging from about 1°C to 27.2°C, but in terms of effort frogs were captured with greatest facility in water ranging from about 10°C to 26°C (Table 11). Probably in colder water the frogs are inactive and lie concealed on the bottoms of pools, and in warmer water (more than 26°C) there is a tendency for them to move to other pools. Sampling at different times of day shows that frogs are most active between the hours of 1 p.m.

TABLE 11. Variation in activity of *Rana p. pretiosa* as judged by facility of capture under varying temperature conditions.

	WATER TEMPERATURE (°C)					
	0-4.4	4.5-10.0	10.1-15.6	15.7-21.2	21.3-26.7	26.8+
Total minutes expended in sampling.....	60	665	1150	1620	720	200
Total frogs captured or observed.....	15	160	413	669	260	48
Frogs/minute.....	0.25	0.24	0.36	0.41	0.36	0.24

TABLE 12. Variation in activity of *Rana p. pretiosa* as judged by facility of capture at different times of day.

	TIME OF DAY										
	A. M.		P. M.					A. M.			
	6-9	9-11	11-1	1-3	3-5	5-7	7-9	9-11	11-1	1-3	
Total minutes expended in sampling.....	40	385	1445	1580	740	565	30	230	205	40	
Total frogs captured or observed.....	7	81	398	606	267	216	9	68	53	5	
Frogs/minute.....	0.18	0.21	0.28	0.38	0.36	0.38	0.30	0.30	0.26	0.13	

and 7 p.m., the times of maximal water temperatures (Table 12).

Twenty-five cloacal temperatures ranged from 5.5°C to 37.8°C. The relationship of the cloacal temperatures to the temperatures of the water in which, or the substrates on which, the frogs were taken is illustrated in Fig. 14. There is a close correspondence between these temperatures but the cloacal temperatures are usually slightly higher.

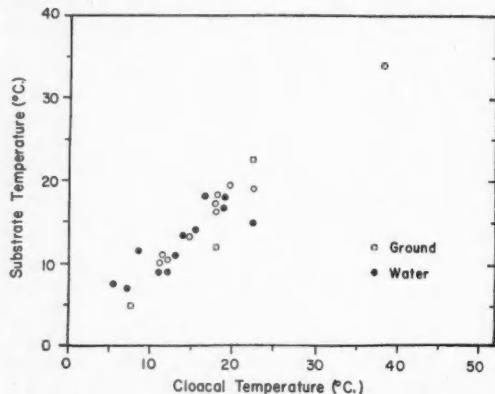


FIG. 14. Relationships between the cloacal temperatures of 25 *Rana p. pretiosa* and substrate temperatures.

Low temperatures, i.e. below 10°C, inhibit activity and hence movements, while water temperatures above 26°C promote movement to other areas. There is little nocturnal activity by frogs, except during the breeding season, and I consider this to be a corollary of low night temperatures. It may also be inferred that the lower growth rates at the beginning and end of the growing season are associated, at least in part, with a curtailment of feeding activity brought about by lower temperatures. Martof (1956a) has pointed out a similar correlation between rate of growth in *Rana clamitans* and the number of hours above 15.6°C.

SUMMARY

1. The growth rate of the Lake Lodge frogs is very low compared to rates revealed by studies of other anurans. The pre-reproductive life span is almost 4 yrs in males, 5-6 yrs in females. The annual growth increment decreases each year so that the average growth during the first full year after transformation is about 10 mm, during the second year about 7 mm, during the third about 6 mm, and during the fourth about 3 mm. The rate of growth of older frogs is very low—probably the annual increments are on the order of 1 or 2 mm or less. There is seasonal variation in the rate of growth and the maximal growth occurs during a 2-3 week period in July. The population is sexually dimorphic with respect to body length; females are larger.

2. The Lake Lodge population inhabits a marginal area and replacement is spotty, even virtually nil in

some years because of almost complete larval mortality. The age composition of the population varies from year to year and the size of the various year-classes reflects varying degrees of reproductive success in past seasons. The mortality rate is approximately the same for all year-classes (about $.39 \pm .10$ over the period of time studied) and survivorship curves for males and females are, insofar as can be determined, Type II or diagonal. The sex-ratio is about 1:1 through the 5th year after transformation but there are approximately 3.5 times as many older females as older males in the population (or there is a persistent sampling bias creating an illusion of such a situation). The inconsistency between the observed numbers of old males and females and the apparent absence of differential mortality is not explained, though a hypothesis postulating increased mortality in males at the end of 5 yrs is advanced. Predation pressure is very light, at least insofar as adult frogs are concerned. Marsh hawks, occasional vagrant garter snakes, and possibly a few mink are the only members of the community which emerge as likely predators. Tadpoles are eaten by dytiscid larvae and several passerines (robin, grey jay) but the conditions which promote predation by birds also result in tremendous larval mortality, owing to desiccation, so that avian predation on tadpoles probably does not affect population size markedly. The size of the Lake Lodge population is estimated at around 1587 in 1953. The mortality-emigration ($.39 \pm .10$) of about 600 between 1953 and 1954 was approximately offset by recruitment of young (about 555) from the 1953 breeding effort. The mortality between 1954 and 1955 is estimated as approximating that of 1953-54 (estimates of $.47 \pm .18$ and $.30$ by two different methods). The 1954 reproductive effort contributed from 35 to 50 young so the population is estimated to have declined to about 1000 individuals in 1955.

3. The population exhibits marked changes in dispersion during the summer and these changes are associated with migrations of the population to upland situations in May and a return to permanent water in July. All members of the population participate in these movements and there are no differences between the sexes or age-groups with respect to rate or magnitude of movements. However there are differences in the types of upland habitats utilized. Sexually mature frogs occupy ponds where oviposition is to occur while younger frogs occupy other habitats, e.g. small puddles in the meadows and intermittent stream courses. Emigration to adjacent stream systems occurred; a maximal movement of 4200 ft was recorded. The location of physiographic features in the area determines the pattern of movements and influences the size of activity ranges. It was found that frogs occupying three different sections of the study area exhibited activity ranges differing significantly in extent.

4. The amount of precipitation influences the rate of disappearance of transient pools and the timing of the return of the population to Soldier Creek. The greatest activity of frogs was found to occur when water temperatures ranged from 10°C to 26°C and the diel pattern of activity, which exhibited a peak between 1 and 7 p.m., is apparently correlated with the more favorable water temperatures existing at this time.

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VEGETATION OF THE SISKIYOU MOUNTAINS, OREGON AND CALIFORNIA¹

R. H. WHITTAKER
Biology Department, Brooklyn College, Brooklyn 10, N. Y.

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I. INTRODUCTION

NATURE OF THE STUDY

The Klamath Region, between the southern Cascade Range and the Pacific Ocean in southern Oregon and northern California, is an area of exceptional ecological interest. These old and geologically complex mountains support an exceedingly complex pattern of natural communities in relation to steep climatic gradients and diverse parent materials, and among these communities a prevailing climax, the Mixed Evergreen Forest, which has a central relation to other western forest vegetation. One area of the region, the Siskiyou Mountains along the California-Oregon border, was selected for vegetation study. Quantitative samples were taken over a wide range of topographic situations, climates, and parent materials for gradient analysis, seeking to relate distributions of plant populations and characteristics of communi-

ties to environmental gradients. Analysis and interpretation were based on the conception of the vegetation as a multi-dimensional pattern, and on study of the manner in which local patterns of vegetation in relation to topographic moisture gradients change along climatic gradients and from one parent material to another. The sections which follow include vegetation description, climax interpretation, community classification, floristic analysis, and consideration of species distributions for the pattern of Siskiyou forest vegetation in relation to four major environmental gradients—local topographic moisture, elevation, the diorite-gabbro-serpentine series of parent materials, and the east-west climatic gradient from the Pacific Coast inland.

GEOLOGY

The dominating topographic features of the Pacific Coast states are the two chains of mountains which run parallel to the Coast from Canada to southern California, and the chain of valleys between them. The higher, inner mountain chain is formed by the Cascade Range and the Sierra Nevada; the lower, outer chain includes the "Coast Ranges" in a

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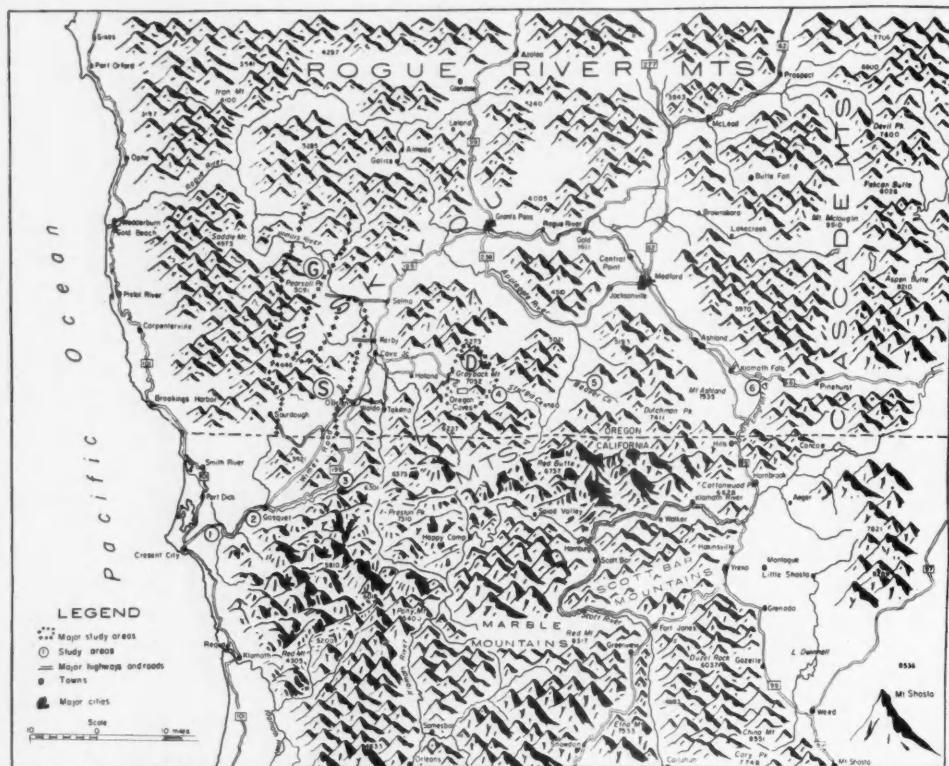


FIG. 1. Map of Siskiyou Mountains of California and Oregon in relation to other, adjacent ranges. Major study areas on three parent materials within the Mixed Evergreen Forest Region are outlined and marked with circled letters: (D) the diorite area, (S) the serpentine area, (G) the area of gabbro and hornblende diorite. Study areas for the west-east climatic transect from the Coast inland are marked with circled numbers: (1) Mill Creek State Park (Sequoia forest), (2) South Fork, Smith River (coastal Pseudotsuga forest), (3) Siskiyou Fork, Smith River (mixed evergreen forest, more mesic phase), (4) Sturgis Creek (mixed evergreen forest), (5) Beaver Creek (mixed evergreen forest, more xeric phase), (6) Emigrant Creek (oak woodland, with Pseudotsuga forest in most mesic and valley grassland in most xeric sites).

broad sense. In northern California and southern Oregon a complex of mountains, the Klamath Ranges, extends from the Coast inland to the southern Cascade Mountains and interrupts the chain of valleys between the two mountain chains. Geographically the Klamath mountains are part of the coastal chain; but they differ from the Coast Ranges north and south of them in age and history, in geological character and complexity, in height and east-west extent. Their closest geological relations are not with the Coast Ranges, but with the Sierra Nevada and the older core of the Blue Mountain complex of Oregon (Fenneman 1931).

The Klamath Region, as it was outlined, described, and named by Diller (1894, 1902, 1903, 1906, 1914), extends north and south for about 390 km, and westward from the Cascade Mountains about 120 km, to reach the Pacific Coast between 41° and 43° north latitude, with a total area of about 34,000 km². The Siskiyou Mountains are the northernmost of the

major mountain groups of the central Klamath Region; like other major ranges of the Region, they are a complex area of mountains rather than a well-defined ridge. The Siskiyous extend in an east-west direction along and on each side of the California-Oregon border, north of the Klamath River and south of the Rogue River. From the Pacific Coast they extend inland from low mountains, with elevations less than 1000 m near the coast, through the main area of mountains of intermediate elevations, including some peaks above 2135 m, to the low mountains which connect with the southern Cascade Range.

The older geological history of the Klamath Mountains is essentially the same as that of the Sierra Nevada (Diller 1894, 1903, 1906; Fenneman 1931). Extensive masses of sedimentary rocks were deposited in an inland sea in Devonian and Carboniferous time; and, at the close of the Paleozoic, these and other rocks were folded and raised into mountains. These mountains were worn down, and much of the area

submerged in Triassic and Jurassic time, while additional sediments and volcanic materials were deposited. At the close of the Jurassic, extensive deformation and intrusion occurred, accompanied by another uplift. A long cycle of erosion followed until, during the Cretaceous, the low mountains remaining subsided and were again largely submerged, with deposit of extensive sedimentary rocks.

At the close of the Cretaceous the Klamath Mountains were again uplifted; and they have existed, as at least low mountains, throughout the Cenozoic, with a complex history of uplift, subsidence, and erosion (Diller 1902). Results of this history are to be seen in wave-cut coastal terraces (Diller 1903, Fenneman 1931:463, Dicken 1952) and peneplain remnants (Diller 1902) in the Siskiyou Mountains. One of these, the Klamath peneplain, is of major significance in the study area. Erosion during the early Cenozoic reduced much of the region, by Miocene time, to a surface of low relief above which scattered mountain ranges rose. This peneplain was later subjected to repeated elevation and subsidence, and probably some tilting and deformation. The Klamath peneplain now appears as a dissected plateau, the surface of which in general rises from the Coast inland and from the north to the south. In the Siskiyous it is about 500 m near the coast, but rises to 1200 to 1350 m, 40 to 80 km inland; farther south in the Salmon and Yolla Bolly Mountains remnants appear at 1800 to 2200 m (Diller 1902, Fenneman 1931). In the central Siskiyou area, one may climb onto the peneplain by the Wimer Road and observe its surface in the serpentine and gabbro uplands west of the Illinois Valley. Sighting across the valley one may observe remnants of the surface in the lower, metavolcanic mountains, while the diorite monadnock of Grayback Mountain rises above it to 2148 m.

A great mass of ancient, closely folded and faulted rocks, generally metamorphosed, and intruded by igneous rocks, form the Klamath Mountains (Fenneman 1931). The consequence of their history of sedimentation, vulcanism, and igneous intrusion, uplifting, folding, faulting, and erosion is an extremely complex mosaic of rock types, a mélange of diverse parent materials. Peridotite and serpentine intrusions, characteristic of many mountains and island chains (Hess 1955), are especially extensive and conspicuous in vegetational effect. The deformation of these mountains was due to repeated compression from the east; and the folds thus formed are curved or crescent-like, striking southeast toward the Sierra Nevada in the southern part of the Klamath Region, northeast toward the Blue Mountains in the northern part (Diller 1914, Fenneman 1931). A trend toward the north-northeast is evident in the formations outcropping in the area of the Siskiyous studied (Wells *et al.* 1949, Wells & Walker 1953).

Geologic maps for Siskiyou quadrangles have been published by Diller (1903), Diller & Kay (1924), Maxson (1933), Wells (1939, 1940), Wells *et al.*

(1949), Wells & Walker (1953), and Cater *et al.* (1953). The Kerby and Grants Pass quadrangles (Wells *et al.* 1949, Wells 1940) include the main study areas in the central Siskiyous. In the Grants Pass quadrangle, the most extensive area is underlain by metavolcanic rocks of Paleozoic age; along with these occur a number of larger and smaller outcrops of diorite, thought to represent a single great batholith of Jurassic or Cretaceous age. Of these, the larger outcrop of quartz diorite (about 120 km²) which includes Grayback Mountain served as one study area. Other rocks on which vegetation could be observed in the area included various metasedimentary rocks—the marble in which the Oregon Caves occur, slate, argillite, and quartzite—and serpentine. In the Kerby quadrangle large areas of both serpentines and gabbros occur, together with various metavolcanic and metasedimentary rocks, granodiorite, hornblende diorite, dacite porphyry, and amphibole gneiss. The unmetamorphosed serpentines are predominantly saponite, with small areas of dunite and pyroxenite. The fringes of the main peridotite mass and the smaller outcrops outlying from it are largely metamorphosed into serpentine rock in the narrower sense. The peridotite and serpentine together form a great sheet, thousands of meters but probably not over 4500 m, in thickness intruded along planes of weakness into the other rocks of the area. The study of low-elevation serpentine vegetation was concentrated in the peridotite and serpentine area from Eight Dollar and Josephine Mountains west to Chetco Peak and south beyond Oregon Mountain into California. This, with a north-south extent of 90 km and an area exceeding 700 km², is the largest body of ultramafic rock in the United States and perhaps in North America (Wells *et al.* 1946, Cater *et al.* 1953). The olivine gabbro study area, of about 36 km² including York Butte, is part of a larger belt of gabbro and hornblende diorite (over 260 km²), also intruded in Jurassic or Cretaceous time, lying northwest of but parallel to the serpentine area.

The complex rock pattern and history of the Klamath Mountains have produced no well-defined trend in stream drainage and ridge direction; the Siskiyou Mountains give the impression of ". . . a confusion of broken mountain ridges with steep and stony slopes . . ." (Peek 1941). The principal rivers of the Klamath Region cut transversely across it, running generally westward from the interior valleys, through deep canyons in the mountains themselves, to the ocean (Anderson 1902). Walls of these canyons are long, and often steep, inclines from the upland to the valley bottoms, interrupted in some cases by terraces remaining from past erosion cycles (Diller 1902, Fenneman 1931); valley bottoms are mostly narrow. Mountain slopes with an average grade of 30° or more through a range of 1000 m or more are common; over most of the region rugged mountain topography prevails. Although the Klamath peneplain is represented by rolling uplands in some areas

of the Siskiyous, the mountains of lower elevations are in general stream-eroded to topographic maturity.

Topography of higher elevations of the Klamath Mountains has been shaped by many local alpine glaciers; the description of glacial effects in the Trinity Alps by Hershey (1900) applies as well to the Siskiyou Mountains. Cirques, with steep rock walls with scanty vegetation and floors with tarns and mountain meadows, occur in the Grayback area and other higher mountains; but the fraction of the area showing glacial topography is small. The non-forest vegetation of the glacial topography is outside the concern of the present monograph.

THE CENTRAL RELATION OF THE KLAMATH FORESTS

To the ecologist familiar with both the Southern Appalachians and the Klamath Mountains, there are a number of striking parallels between these regions. Both are old mountains, with land surfaces which have been continuously occupied by vegetation throughout the Cenozoic, at least. Both persisted as monadnocks through major early Cenozoic cycles of erosion, culminating in the Schooley peneplain of the Southern Appalachians, the Klamath peneplain of this region. Both have been refuges for plant populations destroyed in other areas by glaciation, submergence of coastal plains, climatic desiccation, and, in the West, the great lava flows of the Interior. Both contain modern vegetation which is most nearly related to the widespread Arcto-Tertiary forests of the earlier Cenozoic. Both are areas of great vegetational diversity, and also areas of great floristic diversity and concentrations of narrowly endemic species. Both have "central" relations to the forest floras and vegetations of other, surrounding areas.

Figures are not available, but there is no doubt that the flora of the Klamath Region is extremely rich in numbers of species and numbers of narrow endemics for its latitude. Many genera show concentration of high proportions of their species, including endemics, in this area. Many of the endemics appear to be relicts of formerly wider distributions; in other cases species have probably spread from the Klamath Region to other areas of the West. Thus in the genus *Crepis*, a number of diploid species are now relict in the Klamath area, while genetic material from these has been used in apomictic polyploids which have spread over semi-arid environments of the Interior (Babcock & Stebbins 1938). The region possesses also a greater diversity of forest communities, in a more complex vegetation pattern, than any comparable area of the West. With the exception of more typical forms of the Pigmy Conifer Woodlands, all the plant formations dominated by trees of the western United States occur there, as they do in no other area.

Three interrelated reasons for this central relation may be given on the basis of the vegetational history of the West, the geological history and characteristics of the mountains, and their location. In

broadest statement, the history of western forests from Miocene time to the present has been one of progressive shrinkage toward the Coast and higher elevations, accompanied by progressive differentiation in the different areas of the West, while the diverse floristic elements of the Madro-Tertiary Geoflora were progressively expanding and differentiating in the Southwest and the drier lowlands of the Interior (Chaney 1947, 1948, Axelrod 1958, 1959). Forests most suggestive of the mixed forests of the Miocene are now restricted to the Southern Appalachians in the East, the Klamath Region and coastal California in the West. It is in these two areas that the combination of sufficiently favorable moisture conditions with sufficiently warm temperatures permit the existence today of remnants of the Arcto-Tertiary Geoflora. The significance of the Southern Appalachians in relation to the eastern forests has been extensively developed by Braun (1935, 1938, 1947, 1950).

A second basis of the central relation of the Klamath Region is in its climatic, topographic, and edaphic diversity, together with the age of the mountains. Climatic variation and topography permit a wide range of communities to exist in the region and in different situations in a given area. The different parent materials also have striking effects on floristic and vegetational diversity. Many of the narrowly endemic species in which the region is so rich occur on serpentine, gabbro, or other localized parent materials. Parent-material differences make possible also much of the distributional overlap in the region of species with diverse geographic relations. Thus, in the central Siskiyous, *Taxus brevifolia* in the southern part of its distribution occurs on diorite, *Pinus ponderosa* near the western limit of its distribution on gabbro, and *Pinus jeffreyi* near the northern limit of its distribution on serpentine; these three species appear in the same limited area, but not in the same stands.

The diversity of habitats has been characteristic of the area throughout its long history, although climatic gradients were probably less steep before middle Pliocene time. Even at the maximum development of the Klamath peneplain, mountains of diverse parent materials existed in the area. The region has at all times offered a complex mosaic of habitats, permitting species of diverse environmental requirements to persist in the area while changing climates eliminated some species elsewhere, and caused others to migrate north or south from the range, or to become largely restricted to the Interior east of the range, while leaving relict populations in the Klamath Region.

Finally, it may be observed that the location of the region makes it the meeting ground of floras of diverse climatic relations. In it the flora which may be broadly termed "Northwestern" meets part of the "Californian" flora, with representation also of the floras of the arid Interior and interior mountains. The Mixed Evergreen Forest climax itself is the

link between the coniferous Coast and Montane Forests on the one hand, and the broad-sclerophyll vegetation of California and Oregon on the other. More than any other area, the Klamath Region is central to the forest floras and forest vegetation of the West.

CLIMATE

The location and topography of the Klamath Region imply a wide range of climatic conditions, including steep climatic gradients from the Pacific Coast inland (Engelbrecht 1955). Coastal climates are strongly maritime, with high precipitations and humidities, abundant fog, limited ranges of temperatures, and low temperatures for their latitudes. The mountains paralleling the coast limit the extent of the maritime influences inland, and produce rapid climatic change toward drier, warmer, and more continental conditions in the interior valleys. Isopleths of January and July temperatures, annual range of temperature, annual precipitation, and relative humidity and evaporation, all tend to parallel the coast (Visher 1954). Kendrew (1937) observes of one aspect of these climatic gradients, that the contrast in temperature conditions between the coast at San Francisco and the Great Valley of California is as great as that between Scotland and North Africa, although the distance is only about 120 km.

Climatic data available for the Siskiyou Mountains themselves (Bowie 1934, Wells 1936, 1941, Sprague 1941) are summarized in Table 1. The stations are arranged in two sequences from the coast inland in California and in Oregon. Mean annual temperatures for low elevations in these mountains are rather consistently around 11.0-11.5°C. Average temperature conditions of valley stations are much the same throughout the area; but the inland stations are at higher elevations, and temperatures at comparable elevations are consequently warmer in the interior than on the coast. More marked contrasts appear in ranges of temperature. Mean monthly temperatures for January decrease from about 8.0° to 1.0-3.0°C, while those for July increase from about 15.0° to 21.0-23.0°C. The difference between these mean monthly temperatures, as an indication of the gradient from more equable maritime toward more variable continental climates, increases from about 7.0° on the coast to 19.0-21.5°C in the interior valleys. Similar trends may be observed in the extreme temperatures given in Table 1.

Mean annual precipitation decreases strongly from the coast inland, from values over 180 cm, through values of 80 to probably 150 cm in the central Siskiyous, to values below 50 cm in the interior valleys. The data for Waldo, in the Illinois Valley between the principal study areas, bear most directly on the work in the central Siskiyous. Siskiyou Summit is in the low mountains connecting the Siskiyous with the southern Cascade Range, and is thus not a part of the low-elevation sequence.

All the stations have maritime patterns of seasonal distribution of precipitation, with heaviest rainfall in

TABLE 1. Climatic data for stations at low elevations in the Siskiyou Mountains, from the Coast inland in California and Oregon.

		Distance from Coast, km	Elevation in m	Mean annual temperature, °C	Jan. mean monthly temperatures, °C	July mean monthly temperatures, °C	Min. extreme temperatures, °C	Max. extreme temperatures, °C	Growing season in days	Annual precipitation, mm.	Per cent of precipitation in summer (4 mos., June-Sept.)	Annual snowfall, cm
California												
Crescent City	...	16	38	11.3	7.7	15.2	-7	39	230	193	6.5	
Happy Camp	...	64	700	3.2	22.1	-14	45	159	105	3.9	66	
Scott Bar	...	92	549							63	6.0	
Yreka	...	122	801	10.8	1.0	22.0	-22	44	129	44	9.5	42
Montague	...	130	747	11.7	1.0	22.6	-26	43	141	31	14.9	24
Oregon												
Brookings	...	10	37	11.3	7.9	14.6	-8	38	269	187	8.9	3
Buckhorn Farm	...	49	396	11.3	4.1	20.1	-14	42	150	180	3.9	65
Waldo	...	47	503	10.3	2.4	19.5	-17	43	155	126	5.8	84
Williams	...	80	457	11.1	3.7	19.4	-16	42	145	81	6.3	48
Grants Pass	...	88	287	11.8	3.9	21.1	-18	45	132	74	6.5	22
Jacksonville	...	106	500	11.4	2.6	21.6	-18	41	190	67	8.8	32
Talent	...	118	480	11.6	2.9	21.7	-17	42	170	42	13.6	21
Ashland	...	124	601	11.4	3.3	20.8	-17	41	182	50	12.8	45
Siskiyou Summit	...	130	1363	0.6	18.3	-21	38			83	9.8	

winter, December and January, lightest in summer, July and August. The area is in the transition between the two Pacific Coast types of rainfall regime (Ward 1925, Kendrew 1937), the North Pacific with its limited summer rain and the California type with its practically rain-free summers. At Waldo the four months from November to February include 65% of the rainfall, the four months from June to September 6%. Maritime fogs, or low stratus, are a prominent feature of the coastal climate, where fog may be present 50% of the summer hours and where fog and fog-drip from trees contribute significantly to the humid conditions of the redwood belt (Cooper 1917, Byers 1953, Patton 1956, Oberlander 1956). Relative humidities may be assumed to decrease, and evaporation, hours of cloud-free sunlight, and diurnal temperature range to increase toward the interior; but data are not available.

In general character the climates of low elevations in the Siskiyous are warm-temperate, summer-dry, "Mediterranean" climates; corresponding to these climates, plant communities in which broad-leaved evergreen or sclerophyllous trees are prominent prevail over most of the range. The climates of these forests, and especially those of the redwood belt, are considerably more humid than those of Mediterranean Europe. Russell's (1926) application, with modifications, of the Köppen (1900, 1923) system recognized a mesothermal humid belt with equable temperatures near the coast (Csn), a belt of mesothermal humid, Mediterranean sclerophyll climates (Csb) inland from this, and warmer and drier woodland and steppe (Csa and Bsh) climates in the inner valleys, while microthermal climates occur at higher elevations. The Thornthwaite (1931, 1948) systems recognize a sequence from wet or perhumid conditions near the coast through humid in the main area of the range

to subhumid in the interior; low elevations of the area are microthermal by the criteria of the earlier system, cooler mesothermal by those of the later.

The work in the central Siskiyous had as one objective the comparison of vegetation patterns on three parent materials in the same climate. So steep are the climatic gradients across the Siskiyous that the three study areas on diorite, gabbro, and serpentine cannot have the "same" climate. They are all, however, in the same area of the central Siskiyous, represented approximately by the Waldo data. They are thought to be close enough to be reasonably comparable, and the consistency of the vegetational contrasts on these parent materials in different areas of the Siskiyou Mountains supports the conclusion that effects of parent materials far overshadow those of climate in the study areas.

CULTURE AND DISTURBANCE

The rugged topography and generally infertile soils of the Klamath Mountains have not offered resources which would draw a large population into the region. The largest city within the region is Medford, with a population somewhat over 19,000; most of the region is sparsely settled, and much of it is mountain wilderness. The greater part of the area is in National Forest land. The central and western Siskiyous of Oregon, in which most of the study was carried out, are within the Siskiyou National Forest, the eastern Oregon Siskiyous in the Rogue River National Forest. Extensive wilderness areas have been set aside in the Yolla Bolly, Salmon and Trinity Alps, and Marble Mountains; and small areas of the coastal redwood forests are protected as parks. In the Oregon Siskiyous the Oregon Caves National Monument includes typical mountain vegetation of the central Siskiyous, and an area of forests farther east is protected by the Mt. Ashland watershed. Two larger areas of the western Siskiyous are maintained by the Siskiyou National Forest as the Illinois Canyon and Kalmiopsis Limited Areas.

Only limited farming is carried on in the Klamath Region, although the upper Rogue River Valley is an important fruit-growing district. Parts of the Klamath Region are used as range land, although the forests of most of the region provide little food for stock. In the Siskiyou study areas, limited grazing in the forest lands of the serpentine areas seems not to have damaged their vegetation; limited grazing in the higher elevations of the diorite area has severely affected some of the drier mountain meadows. Gold was discovered in the Siskiyous in 1851 or 1852, and the local gold rush brought thousands of miners into the Galicee-Kerby-Waldo area which includes the serpentine and gabbro mountains studied. Diller (1914, see also Diller & Kay 1909, Maxson 1933, Shenon 1933, Wells *et al.* 1940, 1949) mapped and described 52 placer mines and 67 lode mines and prospects in this area. Little more than marginal mining is carried on in the area now; and the mining settlements of Gold Rush times have shrunk to vil-

lages, or to fields with few vestiges of the old buildings.

Lumber now forms the principal resource and industry of most of the Klamath Region. The coastal redwood belt contains immensely valuable timber lands; within the central Siskiyous Port Orford cedar (*Chamaecyparis lawsoniana*), Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), and to a lesser extent other species, form valuable timber stands. Lumbering practice at low elevations generally involves removal of the conifers of the mixed evergreen forests, leaving at least partial sclerophyll cover. With the relative depletion of more available timber farther north and consequent shift of lumbering activity toward the south, much of the forest area of the Siskiyous is being rapidly cut; and conservation and sustained-yield programs are little in evidence (Dicken 1952).

In the dry-summer climate of the Siskiyous, the forests are easily set afire; and fires of widely varying intensities have been frequent. The Klamath and other Indians are believed to have set fires in connection with hunting and warfare. In Gold Rush days and thereafter, fires were set prodigally, unintentionally from neglected camp-fires and intentionally to make travel easier, to clear the ground for prospecting, and for recreation. Miners are said to have set fires to enliven an evening's drinking with a mountain slope in flames. Fires were used to drive game, and there is a report of a successful hunt that bagged 18 elk through the destruction of 3 billion feet of timber (Forest Service 1940). Probably all lower-elevation mixed evergreen forests have been affected by less intense fires in the litter and undergrowth, at least; and most forests of higher elevations have been burned at some time (cf. Leiberg 1900).

LITERATURE

There are apparently no published studies of the vegetation of the Klamath Region, except the author's (Whittaker 1954b) earlier account of low-elevation diorite and serpentine vegetation in the Siskiyou Mountains. Brief descriptions of the Klamath Region are given by Harshberger (1911), Peck (1925, 1941), and Munger *et al.* (1926). Jepson (1923-5, 1935), Mason (1927), Peck (1941), and Detling (1948b) have commented on the concentration of narrowly endemic species in this region. Vegetation descriptions of other areas most pertinent to interpretation of the Siskiyou vegetation include Cooper (1922) on the broad-sclerophyll vegetation of California, Munz & Keck (1949, 1950, 1959), Jensen (1947), and Burcham (1957) on California vegetation types, Shreve (1927), Clark (1937), Bowerman (1944), and Sharsmith (1945) on the California Coast Ranges, Baker (1951), Merkle (1951), and Detling (1953, 1954) on the Oregon Coast Ranges, Grinnell & Storer (1924), Klyver (1931), and Oosting & Billings (1943) on the Sierra Nevada, Grinnell *et al.* (1930) on Mt. Lassen and Merriam (1899) and Cooke (1940, 1941,

1955) on Mt. Shasta, Becking (1956) on the Douglas-fir forests of the Northwest, and Hansen (1947) on northwestern vegetation and forest history.

The foreign studies most relevant to the present work are two studies dealing with vegetation of serpentine and normal soils and the mafic soils which are intermediate to them (Sočava 1927, Pichi-Sermolli 1948). General characteristics of serpentine vegetation as they appear in the Siskiyous and other parts of the world were reviewed by the author (Whittaker 1954a, 1954b); and this work includes (together with additional European papers cited by Novák 1923, Pichi-Sermolli 1948, and Rune 1953) a bibliography of world literature on serpentine vegetation. Citations which should be added to it are discussions of Balkan serpentine by Beck (1901) and Adamović (1909), an account of grass and herb communities on serpentine in an area of heath in Shetland (West 1912), descriptions of grassland and pine communities on serpentine in Hungary (Soó 1934, Zólyomi 1936), mention of the effect of gabbro in Greenland by Böcher (1933:13), and observations in Switzerland by Lüdi (1937) and in the California Coast Ranges by Sharsmith (1945). The extensive recent literature includes material on serpentine vegetation in Germany (Gauckler 1954) and Austria (Eggler 1954), Bosnia and Serbia (Ritter-Studnička 1953, 1956, Pavlović 1953, 1955, Krause & Ludwig 1956, 1957, Krause & Klement 1958), Scandinavia (Knaben 1952, Rune 1954b, 1954c, Kotilainen & Seivala 1954), Italy (Gismondi 1953), Cuba (Smith 1954), New Caledonia (Baumann-Bodenheim 1956), Japan (Yamanaka 1954, 1955, 1956, 1957, Hattori 1955, Taniguti 1958), Great Britain (Steele 1955, Coombe & Frost 1956a, 1956b, Spence 1957), Quebec, (Rune 1954a), and California (McMillan 1956). The basis of serpentine infertility has been discussed by Hunter & Vergnano (1952), Vergnano (1953a, 1953b), Minguetti & Vergnano (1953), Martin *et al.* (1953), Walker (1954), Kruckeberg (1954), Walker *et al.* (1955), Crooke (1956), Tadros (1957), and Krause (1958).

Taxonomic references used included Jepson (1923-5), Peck (1941), McMinn & Maino (1937), McMinn (1939), and Abrams (1940-51). Of these Peck (1941) applies most directly to the very localized flora of special parent materials in southwestern Oregon, where much of the study was carried out. Most plant names are in the form given in Peck's manual; names not included in it, or given here in a different form, are accompanied by authors' names where first mentioned. The more recent manual of Munz & Keck (1959) also includes most of the flora of the study areas.

II. PROCEDURE

STUDY AREAS

The quantitative part of this study deals with relations of plant populations, vegetation patterns, and floras to: (1) topographic moisture gradients from ravines to south-facing slopes, (2) elevation, on a

more typical soil parent-material in the central Siskiyou Mountains, (3) the parent-material series from diorite through gabbro to serpentine, in the central Siskiyou Mountains, and (4) the climatic gradient from humid-maritime to drier and more continental climates, from the Pacific Coast inland along the California-Oregon border. Within each elevation belt, parent material, and location along the maritime-continental gradient, samples were taken to represent the topographic moisture gradient. The study is based primarily on the comparison, not of individual communities or community-types, but of moisture-gradient patterns of vegetation as these change in relation to elevation, parent material, and the east-west climatic gradient.

The area of most intensive study was in the quartz diorite mountains lying behind Oregon Caves National Monument and including Grayback Mountain. This and the other study areas in the central Siskiyous may be reached by side roads leading from the series of villages (Kerby, Selma, Cave Junction, and O'Brien) along U. S. Highway 199 in the Illinois Valley in southernmost Oregon, back into the mountains east and west of the valley. The diorite area is best reached from the Oregon Caves, at the end of a road leading from Cave Junction, and a branch from this road up Grayback Creek. About 290 vegetation samples, from elevations between 550 and 2100 m, were taken from this area in the summer of 1949.

Study of effects of parent material was made possible by the existence, across the Illinois Valley, 27 km west and 52 km northwest from the diorite area, of extensive outcrops of serpentine and gabbro. These three rocks are part of a major gradient in characteristics of parent materials, represented by the sequence of intrusive, igneous rocks from acid or felsic granite, through intermediate diorite, to basic or mafic gabbro, and ultrabasic or ultramafic serpentine. No granite was available for study close to the other areas. The main area of serpentine studied is accessible on the historic and scenic Wimer Road leading southwest from O'Brien across Oregon Mountain, and other side roads leading into Rough-and-Ready Creek, Tennessee Mountain, and Eight-Dollar Mountain. The gabbro area of York Butte is accessible by a trail to York and Panther Creeks from the end of a minor road leading west from Selma to Oak Flat. The serpentine sampling was carried out in the summers of 1949 and 1950, the gabbro sampling in the summers of 1950 and 1951. These serpentine and gabbro areas are low mountains, mostly not extending above the level of the Klamath peneplain (about 1200 m). The serpentine samples from this area were supplemented with samples from various other, smaller outcrops from all elevations in different parts of the Siskiyou Mountains.

For the study of vegetational gradation from the coast inland, more limited sample series were taken at low elevations on more typical parent-materials in six areas from coastal redwood forest inland to an in-

terior valley. Locations of these areas and their vegetation will be described in Part IV. Limited series of vegetation samples were taken also from a number of other parent materials, mainly metavolcanic rocks, marble, slate, argillite, and quartzite in the Oregon Caves area, from high-elevation forests in other areas of the Siskiyous, mainly near Ashland Peak and Preston Peak, and from successional communities. The study as a whole is based on 470 formal vegetation samples, of the type to be described, and supplementary field notes and plant collections.

VEGETATION SAMPLES AND SOIL DATA

As the basis of the gradient analysis 60 vegetation samples, representing the full range of moisture-gradient conditions within elevation belts of 1000 ft or 300 m, were sought from each of the three rock types at low elevations, and from all elevation belts on diorite. Within a given area of relatively undisturbed vegetation, the author and field assistant walked over the mountain surface without set plan, but usually either following a contour line or ascending a slope vertically. In the former case samples were taken from each new site or slope exposure which seemed favorable for sampling; in the latter case samples were taken at 200-ft (61 m) intervals of elevation. In either case actual location of samples was subjectively chosen—only stands were sampled which seemed of sufficient area and homogeneity and in reasonably undisturbed condition. After 40 of the 60 samples for an elevation belt were taken, the last 20 samples were, if necessary, selected to obtain a reasonably even representation of the different types of topographic sites.

Vegetation samples were based upon a 50-m steel tape, normally laid out perpendicular to the contour lines. All tree stems were recorded by diameters in a strip extending 10 m on each side of the tape. This tenth-hectare sample was supplemented by an additional tenth hectare between 10 and 20 m on each side of the tape, when stands were open or highly mixed, but sufficiently homogeneous to permit such expansion of the sample. Tree seedlings, shrubs, and herbs were counted in 25 one-meter-square quadrats; these quadrats were the alternate square meters along one side of the 50-m tape. To provide density as well as frequency information, an effort was made in all cases to count individual plants in the square meters, even though such counts have limited meaning for some plant species. When additional information on shrub or seedling populations was desired, a count of individual plants was made in a strip 5 m on each side of the tape. In stands with sparse herb growth the herb-layer samples were sometimes expanded to 50 sq m along the tape; and in all samples species observed outside the quadrats were recorded. Coverages were determined by recording the presence or absence of herb and shrub (and in more open stands, tree) cover at the 100 points which marked the corners of the 25 sq m undergrowth quadrats. Location and

environment, and evidence on fire-history were also recorded.

The most extensive work in gradient analysis in this country, apart from the author's, has been that of the Wisconsin group (Cottam & Curtis 1949, 1955, 1956, Curtis & McIntosh 1951, Brown & Curtis 1952, Hale 1955, Culberson 1955, Curtis 1959), using forest samples based on random pairs of tree stems from relatively large areas of more level terrain. The type of sample developed by the author for the present study is adapted to mountain topography, where a sample concentrated within a more limited area is needed. For the present study the sample based on the 50-m steel tape was considered effective, reasonably rapid, and easily adapted to the variety of vegetation types studied.

An effort was made to collect herbarium specimens of all species dealt with in the study in sufficient numbers to represent different habitats in which the species occurred. The herbarium collection was determined, except for some groups sent to other specialists, by M. Ownbey and A. Cronquist; and the voucher specimens of mature plants were placed in the Herbarium of Washington State University.

Soil samples were collected from 15 stations, 5 from different topographic situations within each rock-type, to compare inorganic nutrient conditions in soils developed from the three parent materials. Analyses were carried out in the soils laboratory at Washington State University; a summary of the results is given in Table 2. The "xeromorphic" char-

TABLE 2. Soil analyses for three parent materials at low elevations in the central Siskiyou Mountains. Values are averages of 5 samples representing different topographic situations on each parent material.

	Quartz diorite	Olivine gabbro	Serpentine
Cation exchangeable capacity, m.e./100g.....	21.7	31.8	21.2
Exchangeable cations, m.e./100g: Calcium.....	9.8	7.9	3.3
Magnesium.....	2.6	2.6	13.0
Potassium.....	0.56	0.48	0.12
Sodium.....	0.29	0.28	0.30
Hydrogen.....	15.3	22.7	9.5
Soil Acidity (pH).....	5.8	6.0	6.5

acter of serpentine vegetation (Whittaker 1954b) suggested to the author the desirability of comparing levels of available soil moisture in soils of the serpentine and diorite areas. On two occasions, in 1949 and 1951, series of soil samples were taken from different topographic sites in the two areas to determine moisture content by drying at 105°C. No significant differences between the two areas were established.

ARRANGEMENT OF SAMPLES IN TRANSECTS

The study of Siskiyou vegetation patterns is based on the premise that within each parent material, at

a given elevation in a limited area, one major environmental gradient is of such preponderant effect in determining differences of stable vegetation that other environmental differences may be treated as secondary to it. This gradient is the topographic "moisture gradient" leading from most mesic sites of ravines, through lower, or sheltered, mesic slopes, open north-facing and intermediate (east- and west-facing) slopes to open south- and southwest-facing xeric slopes. Along this gradient, the moisture conditions affecting plants undoubtedly change, but also physiognomy of the vegetation, and other factors of soil and climate, change. The "moisture gradient" is by no means simply a gradient of moisture, and it is not a factor gradient in the usual sense; it is a gradient of whole environmental complexes, a "complex-gradient" (Whittaker 1954c, 1956). It can never be assumed that moisture itself is the cause of an observed species distribution. The study is based, not upon any such assumption, but on accepting the complex-gradient as given, as a basis for ordering samples into transects and comparing vegetation patterns between different parent materials, elevations, and climates.

Since the moisture gradient is not subject to direct measurement in the conditions of this study, other means of arranging samples in sequence along the gradient must be sought. Techniques for ordering samples should, ideally, accomplish two things: (1) They should express, in an effective and sensitive manner, the relative positions of samples along the gradient in question. (2) They should indicate which samples are deviant, departing from the main body of samples along gradients of environment (or disturbance) other than that being studied, gradients which also may be subject to later study (cf. Bray & Curtis 1957). Formal statistical techniques may be adapted to ordering of samples and expression of their directions of interrelation (Goodall 1954a, Hughes & Lindley 1955). In the present study, however, the author has experimented with three less formal, quantitative but nonstatistical, approaches to sample arrangement or "ordination" (Goodall 1954b, *Ordnung* of Ramensky 1930).

The first technique was based directly on topographic relations of sites, and 10 types or groups of sites from most mesic to most xeric: (1) deeper ravines with flowing streams, (2) shallower or more open draws without streams, (3) lower, sheltered slopes, (4) open N-, NE-, and NNE-facing slopes, (5) open ENE and NNW slopes, (6) open E and NW slopes, (7) open ESE and WNW slopes, (8) open SE and W slopes, (9) open SSE and WSW slopes, and (10) open S, SW, and SSW slopes. Samples were grouped by these, into *composite topographic transects* for each elevation belt and parent material.

Topographic position alone is a relatively crude approach to moisture conditions of site. Over-all relations of most plant species to the moisture gradient

are effectively shown by the composite topographic transects, however; and the distributional relations thus indicated were the basis of the second ordination technique, the *composite weighted-average transects*. Species were grouped by the locations of their modes, or maximum population levels, along the gradient, as: (1) Mesic—centered in step 1 or 2, (2) Submesic—in steps 3 to 5, (3) Subxeric—in steps 6 to 8, and (4) Xeric—in steps 9 and 10 of the transect. Lists of species thus classified were prepared for each parent material and elevation belt and used as "ecological groups" (Ellenberg 1948, Whittaker 1954e, 1956) for the ordering of samples in that transect. Population measurements for species were multiplied by weights (the numbers of the ecological groups above); and the total of weighted values was divided by the unweighted total, in the weighted-average technique which was developed independently by Ellenberg (1948, 1950, 1952), Whittaker (1951, 1954c, 1956), Curtis & McIntosh (1951), and Rowe (1956). Bimodal species and those for which the composite topographic transect provided no significant indication of moisture-gradient relations were excluded from the computations.

Tree-stratum and undergrowth weighted averages were computed separately; the values used for the tree stratum were numbers of stems 1 cm dbh or over per 0.1 ha, for the undergrowth numbers of apparent

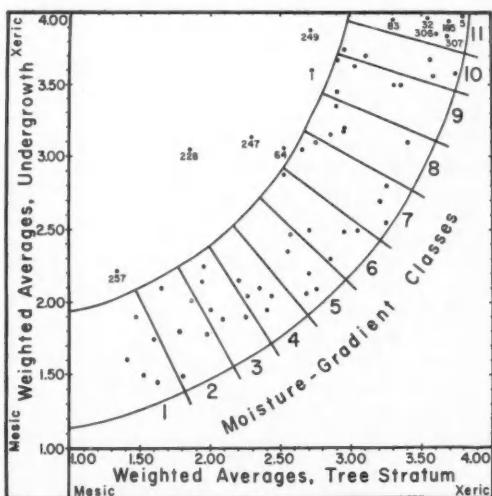


FIG. 2. Weighted-average technique for sample ordination along the moisture gradient. Low-elevation samples from quartz diorite are plotted by weighted averages for both undergrowth and tree stratum, and grouped in 10 classes, or gradient-steps, along the moisture gradient. In this and Fig. 3, numbered samples outside the 10 transect steps are "deviant" from the main body of samples for reasons of parent material, elevation, geographic location, or disturbance. Samples in transect step 11 are sclerophyll stands without *Pseudotsuga*, produced by fires on open south slopes, and more strongly xeric in composition than mature sclerophyll *Pseudotsuga* stands of comparable sites.

plant individuals per 25 sq m. Fig. 2 illustrates the scatter-diagram which results when stands are plotted by weighted averages of the tree stratum on one axis, of the undergrowth on the other. The two values are necessarily correlated; a curvilinear relation such as illustrated results from the manner in which species are assigned to ecological groups. The oblique axis of the scatter-diagram was taken as the best indicator of relative position along the gradient; and in each case 10 segments of the scatter-figure containing 5-7 samples each were marked off, to provide the 10 steps of the transects. Sample deviance is sometimes expressed in wide departure from the axis of the scatter-figure, as indicated by the numbered samples and legend of Fig. 2.

With deviant samples eliminated by this means and judgment, the remaining 50 were grouped into 10 sets of 5 each. Within each set, tree and undergrowth populations were tabulated for areas of 0.5 hectare and 125 sq m, and coverages were averaged. Tree populations were also tabulated separately above and below arbitrary size limits set to distinguish canopy and smaller trees. Compiled tabulations for undergrowth included, for each species in each step of the transect, constancy, frequency, and density; from the data, presence, abundance, and an indication of contagion (Whitford 1949) could also be obtained.

The third series of transects, the *composite sample-comparison transects*, were based on measurement of percentage similarity of samples (see Part VI). If a stand at one extreme of the gradient is taken as a standard, then the degree to which other stands differ from it is in part an expression of their relative distances from it along the gradient. For a more sensitive expression of stand position, all samples of a transect were compared by undergrowth densities with three standards (each an average of 5 stands), (1) most mesic ravines, (2) intermediate, E-facing slopes, and (3) most xeric, S-, SW-, SSW-facing slopes. The resulting percentage similarities for a given stand were weighted from 1 to 3, and the weighted total divided by the unweighted total. The quotient, on the abscissa of Fig. 3, expresses the relation of the stand to the moisture gradient and is used to group the stands into transect steps. The unweighted total, on the ordinate, expresses the affinity of a sample to the main body of sample material as represented in the three comparison standards; low values provide an effective means of recognizing deviant samples.

EVALUATION OF TRANSECT TECHNIQUES

The three types of transects do not give equally satisfactory results, and none gave results as satisfactory as those of the weighted-average technique in the Great Smoky Mountains (Whittaker 1956). The lower sensitivity of weighted averages as moisture-gradient indicators in the Siskiyou is believed to result from the smaller extent of vegetational change along the moisture gradient (see Part VI) and

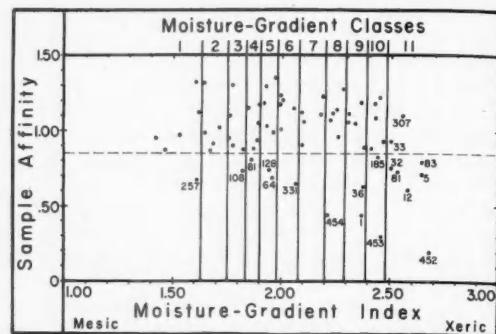


FIG. 3. Sample ordination by comparison with standards. Low-elevation vegetation samples from quartz diorite are plotted by moisture-gradient index (a weighted comparison with samples representing mesic ravines, intermediate open east slopes, and xeric south slopes) and by sample affinity (total of percentage similarities with these three comparison standards, as a measure of floristic consistency with the main body of transect samples from diorite). Samples are grouped into 10 classes, or transect steps, by position along the moisture-gradient index. Samples with affinities less than 0.85 are considered deviant from the main group of samples from low elevations on diorite.

the greater stand-to-stand irregularity resulting from fire. Quantitative indications of relative effectiveness of different techniques of stand ordination are possible, on the basis of certain assumptions about species distributions. It may be assumed, for example, that the more effective the sample ordination, the more each species distribution will be concentrated in part of the transect. Dispersions, or other indications of relative spread of species populations in the transects, may be used as an indication of effectiveness of the ordination technique. Or, it may be assumed that the more effectively is the natural distributional curve of the species represented in the transect, the less will be the irregular, up-and-down difference of population measurements for that species in successive steps of the transect.

In application to the Siskiyou material, lists of species were selected for diorite, gabbro, and serpentine, with the requirements that each species have relatively high population levels for significance of results, and have a distribution extending through several but not all 10 steps of the transects. The number of steps through which a species population extended was then taken as an indication of dispersion or spread; and these values were averaged for the species used to compare transects on a given soil. The sums of signless differences between successive density values in steps of transects for the same species, also averaged for these sets of species, provided an indication of relative smoothness vs. irregularity of the population curves in the transects. In each case, higher values indicate less effective sample ordination. The values obtained for relative spread

of species distributions in the topographic, weighted-average, and sample-comparison transects were: on diorite—8.1, 7.9, 8.2; on gabbro—8.3, 7.7, 8.0; on serpentine—8.7, 7.2, 7.6. Corresponding values for relative irregularities of species distributions in the transects were: on diorite—32.0, 20.7, 23.0; on gabbro—17.6, 15.0, 20.0; on serpentine—34.9, 32.2, 34.7.

TRANSECT TABLES

The main body of transect data for the central Siskiyou Mountains are presented in the following tables, considerably compressed for publication. Distributions of tree, shrub, and herb species in relation to the moisture gradient at low elevations on diorite, gabbro, and serpentine are given in Tables 3 to 11.

TABLE 3. Distributions of trees in a moisture-gradient transect for low elevations on quartz diorite in the central Siskiyou Mountains. Based on 50 stand samples of 0.1 or 0.2 hectares each from elevations between 2000 and 3000 ft (610-915 m) arranged in 10 transect steps of 5 samples each. All values in transect steps are numbers of stems over 1 cm dbh (i.e. from the 0.5-1.5 in class up) or, where indicated, 8 in (20 cm) or 15 in (37 cm) dbh or larger in 0.5 hectare. Transect constancy is the per cent of 50 samples, 0.1 hectare each, in the transect in which the species occurred as a tree over 1 cm dbh.

Transect step	Sites										Xeric Transect Constancy
	1	2	3	4	5	6	7	8	9	10	
Conifers											
<i>Chamaecyparis lawsoniana</i>	102	75	2								22
15 in (37cm) dbh/and over	27	29									
<i>Pseudotsuga menziesii</i>	128	96	153	107	79	78	63	50	86	44	98
15" and over	41	46	50	59	48	54	50	31	42	18	
<i>Pinus lambertiana</i>	1	1	5	2	5	6	3	8	6	44	
15" and over											
<i>Taxus brevifolia</i>	63	53	26	4		1					24
<i>Abies concolor</i>	1	1	2		2						12
<i>Libocedrus decurrens</i>							12				
<i>Pinus ponderosa</i>								1	2		
Sclerophylls											
<i>Lithocarpus densiflora</i>	77	152	483	413	493	473	361	442	399	669	100
8 in (20cm) dbh/and over	11	6	9	3	6	13	18	14	14	34	
<i>Quercus chrysolepis</i>	6	2	87	86	55	102	194	230	325	209	78
8" and over			2	7	21	34	24	12	18		
<i>Arbutus menziesii</i>	2	2	27	50	75	93	124	79	322	68	
8" and over	1	1	4	9	17	40	27	48	13	21	
<i>Castanopsis chrysophylla</i>	23	34	89	79	44	52	11	20	43	162	74
8" and over	1	2		1	3	2	1	3		1	
Deciduous trees											
<i>Alnus rubra</i>	8	2									4
<i>Alnus rhombifolia</i>	9	1									4
<i>Acer circinatum</i>	110	53	185	9	12	2					26
<i>Acer macrophyllum</i>	13	11	14	1	1	4	5				32
<i>Salix</i> sp.	3	1	6	1	5	1	1				18
<i>Cornus nuttallii</i>	35	11	26	34	18	6	8	9	12	7	58
<i>Corylus rostrata</i> var. <i>californica</i>	141	146	58	34	16	11	2	2	4	52	
<i>Quercus kelloggii</i>		3	1		1	1	7	7			18
<i>Amelanchier florida</i>		6									3
Arborescent shrubs											
<i>Philadelphus lewisi</i>	2		2								4
<i>Rhododendron californicum</i>	15	4									4
<i>Holodiscus discolor</i>	9	8	10	8	4	9	14		2		32
<i>Rhus diversiloba</i>											2

These tables are intended to permit direct comparison of distributional relations of species, stand compositions, and vegetation patterns on the three parent materials as the basis of the discussions which follow. Only frequency values for undergrowth species can be given here from the density-frequency-constancy tabulations of the original transects; constancy and density values for the transects as wholes are summarized in the last columns. Distributional relations to elevation on diorite were approached through a series of transects for different elevation belts. In the condensed form given here in Tables 12 to 14 only average population values for whole transects are given for the various elevation belts—density and constancy values of trees and per mille frequencies of shrubs and herbs. Distributions of grasses, sedges, and rushes in relation to both parent materials and elevation are summarized in Table 15.

TABLE 4. Distributions of shrubs and seedlings in a moisture-gradient transect for low elevations on diorite in the central Siskiyou Mountains. Based on 50 undergrowth samples, each of 25, 1-m² quadrats, for elevations between 2000 and 3000 ft (610-915 m) arranged in 10 transect steps of 5 samples each. All values in transect steps are per cent frequencies in 100, 1-m² quadrats (based on 125, 1-m² quadrats per transect step). Transect constancy is the per cent of 50 samples, each of 25, 1-m² quadrats, in the transect in which the species occurred; total density is the number of apparent individuals in an area of 1000 sq m, based on density counts in 1250, 1-m² quadrats in the 10 steps of the transect. Observed presence in samples, outside the first 25, 1-m² quadrats, is indicated by "x."

Transect step	Sites										Xeric Transect Constancy	Total Density
	1	2	3	4	5	6	7	8	9	10		
Conifer seedlings												
<i>Chamaecyparis lawsoniana</i>	2	2										6
<i>Taxus brevifolia</i>	7	2	2	2								15
<i>Pseudotsuga menziesii</i>	2	6			4	9	3	10	12	8	56	70
<i>Pinus lambertiana</i>					2	2		1	1	1		6
<i>Libocedrus decurrens</i>										8		10
Broadleaf tree seedlings												
<i>Acer circinatum</i>	5	2	6	2								18
<i>Amelanchier florida</i>	1		2	2								6
<i>Cornus nuttallii</i>	1		1	1	1							3
<i>Corylus rostrata</i> var. <i>californica</i>	1	9	7	5	3	1	3		1			34
<i>Castanopsis chrysophylla</i>	2	2	6	8	4	1			2	6		38
<i>Lithocarpus densiflora</i>	31	18	27	26	39	28	30	21	34	30		100
<i>Quercus chrysolepis</i>	3	8	6	13	5	20	21	14	14	14		148
<i>Arbutus menziesii</i>										1	4	2
Shrubs												
<i>Rhododendron californicum</i>	2	1										4
<i>Vaccinium parvifolium</i>	3	6		1	1							15
<i>Gaultheria shallon</i>	31	32	19	25	19	10		8				537
<i>Rubus parviflorus</i>	1	4		2	1			1	2			14
<i>Berberis nervosa</i>	42	45	21	26	25	20	14	9	9			632
<i>Berberis pumila</i>	2	1					10	13	2			50
<i>Rubus vitifolius</i>	27	26	6	7	5	20	10	11	19	32		271
<i>Rosa gymnocarpa</i>	8	14	22	32	24	38	27	30	37	43		497
<i>Rhus diversiloba</i>	6	12	15	16	15	49	37	31	38	64		611
<i>Holodiscus discolor</i>		1		2	2							6
<i>Pachystima myrsinoides</i>		1							1			2
<i>Symporicarpus hesperius</i>	3	9		1	1	5						26
<i>Ceanothus integerrimus</i>									x	0		0

TABLE 5. Distributions (frequencies) of herbs in a moisture-gradient transect for low elevations on diorite in the central Siskiyou Mountains. For basis of data see heading of Table 4.

Transect step	Sites										Xeric Transect Constancy	Total Density
	1	2	3	4	5	6	7	8	9	10		
<i>Tiarella unifoliata</i>	6										4	10
<i>Satureja douglasii</i>	2										2	6
<i>Asarum caudatum</i>	1										2	4
<i>Claytonia parvifolia</i>	x										0	0
<i>Tolmiea menziesii</i>	x										0	0
<i>Claytonia spathulata</i>	2	1									4	2
<i>Araea californica</i>	2	1									4	4
<i>Boylea elata</i>	8	1									6	99
<i>Adiantum pedatum</i> var. aleuticum	2	1									4	4
<i>Smilacina stellata</i>	3	2									4	25
<i>Anemone deltoidea</i>	7	4	2	2							16	40
<i>Cephalanthera austinae</i>	x	x	x	x							0	0
<i>Linnæa borealis</i>	27	29	26	17	9						32	316
<i>Trillium ovatum</i>	6	6	8	8	2						32	42
<i>Chimaphila menziesii</i>	2	2	1	2							10	14
<i>Pyrola picta</i>	2	2	2	1							10	10
<i>Senecio bolanderi</i>	6	6	29	14	1		2				24	157
<i>Vancouveria hexandra</i>	1	6	4	2		2	2				22	38
<i>Chimaphila umbellata</i> var. occidentalis	2	4	24	14	13	6	8	1			32	249
<i>Whipplea modesta</i>	8	6	28	22	12	10	3	10	4		44	340
<i>Smilacina racemosa</i>	13	1	4	9	x	x	1	2			22	60
<i>Polyodium muninum</i>	22	26	6	5	2	2	10	2	1		48	102
<i>Viola sempervirens</i>	10	7	12	23	6	9		4	6		42	210
<i>Galium triflorum</i>	3	6	3	6	2	1	1	2	2		32	34
<i>Adenocaulon bicolor</i>	2	1	4	8	5	8	2	9			34	101
<i>Iris chrysophylla</i>	1	1	2	1	1	5	4	2			18	52
<i>Achlys triphylla</i>	22	49	19	36	42	19	18	20	8	2	90	1561
<i>Trientalis latifolia</i>	6	8	29	10	10	16	6	10	17	8	70	402
<i>Goodyera oblongifolia</i>	2	2	7	9	10	7	1	2	1	1	42	81
<i>Pteridium aquilinum</i> var. pubescens	2	7	4	7	12	24	17	28	22	55	72	275
<i>Apocynum cannabinum</i>	5	2	4	10	11	14	22	15	10	26	66	203
<i>Diaporthe hookeri</i>	1	4	15	10	12	9	6	5	4	10	52	106
<i>Loniceria hispida</i>	1	6	8	2	6	13	8	15	2	48	145	
<i>Hieracium albiflorum</i>	1	6	9	8	5	24	6	9	21	2	54	202
<i>Alticaria virgata</i>	x					1	1	x	4	4	2	
<i>Heuchera micrantha</i>	1									2	3	
<i>Equisetum hyemale</i> var. californicum	2									2	5	
<i>Coptis laciniata</i>	14									4	42	
<i>Mitchella repens</i>	1									2	1	
<i>Clintonia uniflora</i>	1									2	2	
<i>Corallorhiza striata</i>	x									0	0	
<i>Campanula esculentaria</i>	2	1	1	4	1					12	41	
<i>Asarum hartwegii</i>	2	x	5	2		5				10	20	
<i>Corallorhiza maculata</i>	x	1			1		1			6	7	
<i>Phlox diffusa</i>	2	3	4	7	2	5	1	10		36	78	
<i>Madia gracilis</i>	1	2		4	1	4	10	5	26	106		
<i>Lathyrus pauciflorus</i>	2	1	1		1	1	1	2		12	10	
<i>Arenaria macrophylla</i>	2									2	2	
<i>Habenaria undulata</i>	1									2	1	
<i>Fragaria vesca</i> var. <i>braceata</i>	1		1			1		1		6	2	
<i>Taraxia kelloggii</i>	x			9	9	7	27	16	20	130		
<i>Collomia heterophylla</i>	1			2	6		3	2	18	81		
<i>Campanula pinnatifida</i>	1	1	6	10	22	18	30	22	48	404		
<i>Pyrola secunda</i>	1									2	1	
<i>Pleurozis fimbriolata</i>	x									0	0	
<i>Boschniakia hookeri</i>	1		1			x	1	6	6			
<i>Cypripedium fasciculatum</i>	x			1	2				4	3		
<i>Osmorrhiza chilensis</i>	2									2	5	
<i>Pearlacea physodes</i>	4				1	13	2	8	31			
<i>Cynoglossum grande</i>					3				2	10		
<i>Claytonia perfoliata</i> var. <i>parviflora</i> (Dougl.) Torr.				1					2	2		
<i>Epilobium minutum</i>					2				2	2		
<i>Galium californicum</i>						2		2	5			

TABLE 6. Distributions (stem densities per 0.5 hectare) of trees in a moisture-gradient transect for low elevations on olivine gabbro in the central Siskiyou Mountains. For basis of data see heading of Table 3.

Transect step	Sites										Xeric Transect Constancy	Total Density
	1	2	3	4	5	6	7	8	9	10		
Conifers												
<i>Chamaecyparis lawsoniana</i>	87	6										12
15 in (37cm) dbh/ and over	6	4										
<i>Pseudotsuga menziesii</i>	56	33	24	30	44	32	24	23	12	10	94	
15' and over	11	13	16	14	10	6	8	2	3			
<i>Pinus lambertiana</i>	38	4	9	18	21	20	45	36	11	21	90	
15' and over	2	3	12	8	6	16	13	3	5			
<i>Pinus ponderosa</i>	46										6	36
15' and over											8	8
<i>Libocedrus decurrens</i>	38										3	36
15' and over											2	3
<i>Taxus brevifolia</i>		3										2
<i>Pinus attenuata</i>											1	2
Sclerophylls												
<i>Lithocarpus densiflora</i>	97	340	308	243	280	79	346	336	332	144	94	
8 in (20cm) dbh/ and over	12	28	8	11	5	10		7				
<i>Quercus chrysolepis</i>	22	190	232	271	179	326	339	339	326	96		
8' and over	2	30	35	60	41	46	22	14	12			
<i>Umbellularia californica</i>	17	69	37	22	26	31	43	17	28	53	54	
8' and over												
<i>Arbutus menziesii</i>	1	49	12	31	15	21	13	5	10		42	
8' and over	17	2	6	9	1							
<i>Arctostaphylos cinerea</i>	31	2		5	47	35	170	397	289	805	56	
8' and over												
<i>Castanopsis chrysophylla</i>		1									1	6
8' and over											3	3
Deciduous trees												
<i>Ailanthus altissima</i>		17										6
<i>Ailanthus rhombifolia</i>			6									4
<i>Salix</i> sp.		15										4
<i>Amelanchier alnifolia</i>		49	3									6
<i>Acer macrophyllum</i>		4	13		1							12
<i>Cornus nuttallii</i>		13	112	13	20	26	2	9	20	4	44	
<i>Quercus kelloggii</i>										3	1	6
Arborescent shrubs												
<i>Rhododendron occidentale</i>		256	152	1						6		16
<i>Rhamnus californica</i> var. <i>occidentalis</i>		50		1	6	7	24	28	23	100	35	48
<i>Garrya fremontii</i>		8	2		2	1	12	2	2	5	26	
<i>Rhus diversiloba</i>		2								17	20	
<i>Vaccinium ovatum</i>		130	61	5	17	107	1	119	23	20	42	48
<i>Holodiscus discolor</i>		7	4		5	2	1	14	6		18	
<i>Ceanothus integerrimus</i>								1	4	8	8	8
Liana												2
<i>Vitis californica</i>								1				

These results are in accord with subjective judgment on the relative effectiveness of the three techniques. The weighted-average technique is consistently superior to the other two in this application. It is consequently the transects based on this technique which are published here (Tables 3-11) and used as the principal basis of describing and comparing vegetation patterns. The other transects, however, have been used as checks on the weighted-average transects in some respects, especially on the bimodality of species populations (Part VII). The sample-comparison technique is not necessarily less sensitive and has some advantages over the weighted-average technique; bimodalities of a number of major species

TABLE 7. Distributions (frequencies) of shrubs and seedlings in a moisture-gradient transect for low elevations on olivine gabbro in the central Siskiyou Mountains. For basis of data see heading of Table 4.

Sites	Metric	Xeric										Transsect	Constancy	Total	Densitv
		1	2	3	4	5	6	7	8	9	10				
Transect step	1	2	3	4	5	6	7	8	9	10	Transsect	Constancy	Total	Densitv	
Conifer seedlings															
<i>Chamaecyparis lawsoniana</i>	4												4	4	
<i>Pseudotsuga menziesii</i>	2	2	4	2	4	2	6	9	8	3	54	46	56	36	
<i>Pinus lambertiana</i>	1	2	2	3	2	2	5	7	8	2	56	36	74	46	
<i>Libocedrus decurrens</i>	1					1	1			2	4	14	8	8	
<i>Pinus ponderosa</i>						1	1			2	6	5	5	5	
Broadleaf tree seedlings															
<i>Alnus rhombifolia</i>	2												2	2	
<i>Alnus rubra</i>	1												2	1	
<i>Amelanchier alnifolia</i>	2												2	1	
<i>Lithocarpus densiflora</i>	2	15	19	11	14	6	11	8	6	8	80	112	96	64	
<i>Quercus chrysolepis</i>	2	13	12	19	10	6	15	6	3	6	74	96	112	80	
<i>Cornus nuttallii</i>	2	1											6	4	
<i>Umbellularia californica</i>	2	1	1	2	2	x	1			1	18	9	18	9	
<i>Corylus cornuta</i> var. <i>californica</i>	1												2	1	
<i>Arctostaphylos uva-ursi</i>						1	2	2	6	8	12	36	34	34	
<i>Castanopsis chrysophylla</i>										1		2	1	1	
<i>Quercus kelloggii</i>										1		2	1	1	
Shrubs															
<i>Holodiscus discolor</i>	2												4	2	
<i>Rubus vitifolius</i>	2												6	2	
<i>Rhododendron occidentale</i>	16	7											12	30	
<i>Gaultheria shallon</i>	9	11	8	3	5		7						18	73	
<i>Rubus parviflorus</i>	3	1				1	2						8	13	
<i>Garrya fremontii</i>	1									x	2		6	2	
<i>Rhamnus californica</i> var. <i>occidentalis</i>	10	5	5	4	9	5	7	14	3	10	60	72	72	72	
<i>Vaccinium ovatum</i>	12	3	2	4	6	5	11	6	5	3	42	66	66	66	
<i>Rhus diversiloba</i>	1	22	27	22	27	30	17	6	18	1	74	353	353	353	
<i>Ribes cereum</i>	1	x	x										2	1	
<i>Berberis nervosa</i>	3	11											4	38	
<i>Symphoricarpos hesperius</i>		2											6	8	
<i>Rosa gymnocarpa</i>		4			1								6	10	
<i>Holodiscus dumosus</i>		2			1	3	2						8	9	
<i>Ceanothus integerrimus</i>		2					1	2					6	5	
<i>Amelanchier gracilis</i>		2			2	2	1	1	1	1	10	7	10	7	
<i>Berberis pumila</i>				2		x							2	6	
<i>Quercus chrysolepis</i> var. <i>vaccinifolia</i>					2	4			1	6			8	8	
<i>Convolvulus polymorphus</i>						2	2	2	4	12			15	15	
<i>Juniperus virginiana</i>									x	0			0	0	

(which could be excluded from the weighted averages) are thought to be the reason for its relative ineffectiveness in the Siskiyou transects.

III. VEGETATION DESCRIPTION

LOW ELEVATIONS ON DIORITE

In general character, the vegetation of low elevations on diorite is a forest of two tree strata—an upper stratum of evergreen needle-leaved trees and a lower one of sclerophyllous broad-leaved trees—forming together a closed canopy. In ravines, dominance of the upper tree stratum is shared by *Pseudotsuga menziesii* and *Chamaecyparis lawsoniana*. Three deciduous broadleaf trees—*Acer macrophyllum*, *Alnus rubra* Bong. (*A. oregona* Nutt.), and *A. rhombifolia*—occur in small numbers among the larger stems. Among the smaller trees, two deciduous species, *Cory-*

TABLE 8. Distributions (frequencies) of herbs in a moisture-gradient transect for low elevations on olivine gabbro in the central Siskiyou Mountains. For basis of data see heading of Table 4.

Transect step	Sites	Meric	Xeric										Total	Constancy	Density
			1	2	3	4	5	6	7	8	9	10			
<i>Boykinia elata</i>		45											10	204	
<i>Boykinia major</i>		6											4	11	
<i>Rudbeckia californica</i>		8											4	23	
<i>Adiantum pedatum</i> var. <i>aleuticum</i>		5											8	13	
<i>Claytonia parvifolia</i>		1											2	1	
<i>Goodeaya decipiens</i>		1											2	2	
<i>Erigeron cerninus</i>		4											2	19	
<i>Luina hypoleuca</i>		1											2	2	
<i>Tofieldia glutinosa</i> ssp. <i>occidentalis</i>		10											4	22	
<i>Darlingtonia californica</i>		5											2	18	
<i>Habenaria sparsiflora</i>		1											2	1	
<i>Peltiphyllum peltatum</i>		6											4	11	
<i>Galium aparine</i>		1											2	1	
<i>Cypripedium californicum</i>		3	1										8	15	
<i>Epipactis gigantea</i>		2	1										4	4	
<i>Woodwardia fimbriata</i>		6	3										9	7	
<i>Schoenolirion album</i>		2											6	6	
<i>Lotus oblongifolius</i>		14		1	3					11			10	70	
<i>Smilacina racemosa</i>		2	2	6	1	2	2	2	4				18	26	
<i>Galium bolanderi</i>		1	x					1	2				12	9	
<i>Polytichum munitionum</i> var. <i>imbricatum</i>		2	23	49	29	26	41	11	7	1			60	290	
<i>Tridentaria latifolia</i>		2		3	1	3	2	7	4	1			26	58	
<i>Pyrola dentata</i>		1		x	5	2	8	6	x				24	67	
<i>Polygonum californicum</i>		12	9	9	16	14	21	17	18	28	29	74	392		
<i>Whipplea modesta</i>		10	31	34	42	22	50	27	31	21	10	88	769		
<i>Lonicera hispida</i>		4	27	39	42	38	34	30	7	15	12	86	508		
<i>Iris chrysophylla</i>		1	3	3	13	7	6	20	18	11	14	64	213		
<i>Campanula pannosanthoides</i>		1	2	4	2	11	1	14	6		1	36	146		
<i>Vancouveria planipetala</i>		3											2	17	
<i>Cheilanthes gracillima</i>		x											0	0	
<i>Achlys triphylla</i>		6	2										6	43	
<i>Sedum oreganense</i>		2	2										4	17	
<i>Arenaria macrophylla</i>		1	1										4	10	
<i>Buchanania hookeri</i>		1		1									4	2	
<i>Asarum hartwegii</i>		2	2	6		x							6	10	
<i>Heuchera micrantha</i>		7	1	3	2	2							14	24	
<i>Diplotaxis hookeri</i>		2	3	5	13	6	2	1					32	46	
<i>Acypnoea pumilum</i>		x			4		1	1					6	8	
<i>Chimaphila menziesii</i>		2	6	2	5	1	1	1					24	29	
<i>Pteridium aquilinum</i> var. <i>pubescens</i>		2	2	2	2	1	4	10	13	12			28	76	
<i>Galium ambiguum</i>		3	7	12	11	34	26	43	34	65	76	908			
<i>Hieracium albiflorum</i>		4	5		1			12		x	14	46			
<i>Pterospora andromedea</i>		x											0	0	
<i>Cheilanthes silvatica</i>		2											2	2	
<i>Erythronium capitatum</i>		1											4	2	
<i>Chimaphila umbellata</i> var. <i>occidentalis</i>		2	2	4									3	8	27
<i>Madia sativoides</i>		2	x										4	9	
<i>Arnica spathulata</i> var. <i>eastwoodiae</i>		2			22	9	14	2	7	9			9	97	
<i>Hieracium bolanderi</i>		1	2	2	2	4	11	9	3				30	85	
<i>Pyrola picta</i> f. <i>aphylla</i>			1										2	1	
<i>Cananthus prostratus</i>		x											2	2	
<i>Lomatium hirsutissimum</i>		1		4	3	18	3	14					18	85	
<i>Anemone quinquefolia</i>			4										3	6	22
<i>Arnica parviflora</i> ssp. <i>parviflora</i>			1	2	12	21	8	15					12	106	
<i>Viola lobata</i>		3	2	5	14	14	6						24	126	
<i>Sidalcea malvaefolia</i> ssp. <i>elegans</i>			2										2	2	
<i>Allotropa virgata</i>			2					14	1	2			12	30	
<i>Monardella odoratissima</i> var. <i>glauca</i>			3	1	1	6	3	9					14	41	
<i>Linnacea borealis</i>					1	18							4	57	
<i>Cordylanthus viscidus</i>					1		1						4	2	

(Table 8 Cont.)

Transect step	Sites										Xeric Transect Constancy	Total Density
	1	2	3	4	5	6	7	8	9	10		
<i>Erigeron foliosus</i> var. <i>confinis</i> .					x	1			1	4	10	
<i>Eriophyllum lanatum</i> .					x	1	1	4	8	5		
<i>Aster brickelliioides</i> .						2	2		4	6		
<i>Xerophyllum tenax</i> .					14	8	2	2	12	70		
<i>Ceanothus pumilus</i> .					2	7	15	14	20	62		
<i>Zygadenus micranthus</i> .					1			2	4	3		
<i>Cynoglossum occidentale</i> .						1			2	1		
<i>Salidago</i> sp.						5	1		8	11		
<i>Monardella villosa</i> var. <i>subserata</i> .							7	9	6	25		
<i>Senecio fastigiatus</i> .						2	2	2	8	12		
<i>Eriogonum nudum</i> .						1		2	4	9		
<i>Phlox speciosa</i> .							1		2	2		
<i>Phlox diffusa</i> .								x	0	0		
<i>Pentstemon azureus</i> sp. <i>azureus</i> .								2	2	2		

TABLE 9. Distributions (stem densities per 0.5 hectare) of trees in a moisture-gradient transect for low elevations on serpentine in the central Siskiyou Mountains. For basis of data see heading of Table 3.

Transect step	Sites										Xeric Transect Constancy	Total Density
	1	2	3	4	5	6	7	8	9	10		
Conifers												
<i>Chamaecyparis lawsoniana</i> .	155	5	2	9							16	
10 in (25 cm) dbh and over.	98	4	1	5								
<i>Pinus monticola</i> .	152	93	209	79	46	204	27				60	
10' and over.	8	4	20	7	3	30						
<i>Pinus lambertiana</i> .	2	23	9	11	25	7	17	1	2		56	
10' and over.	2	9	6	9	11	2	3	1	1			
<i>Pinus attenuata</i> .	12	11	16	48	17	23	37	3	2		38	
10' and over.						1	1					
<i>Pseudotsuga menziesii</i> .	43	61	54	41	52	15	87	21	13		84	
10' and over.	21	43	26	12	20	4	22	9	2			
<i>Libocedrus decurrens</i> .	14	15	26	51	69	51	67	40	48	6	86	
10' and over.	5	6	15	7	13	11	15	10	12			
<i>Pinus jeffreyi</i> .	34	10	34	24	28	65	95	86	108	146	78	
10' and over.	2	2	10	8	3	18	14	39	36	38	6	
<i>Pinus contorta</i> var. <i>murrayana</i> .	1				1	22						
Sclerophyllous trees												
<i>Arbutus menziesii</i> .	7	8			3			7	4	12		
<i>Castanopsis chrysophylla</i> .					15	9			4	4		
Arborescent shrubs												
<i>Rhododendron occidentale</i> .	280									8		
<i>Physocarpus capitatus</i> .	10									2		
<i>Rhamnus californica</i> var. <i>occidentalis</i>	7									4		
<i>Arctostaphylos viscida</i> .	8				9		46	9	336	184	28	
<i>Umbellularia californica</i> .	41		11	3	13	11	10	7	19	24		
<i>Quercus chrysolepis</i> var. <i>vaccinifolia</i>	9					2			1	10	2	
<i>Rhododendron californicum</i> .					3				4	2		
<i>Quercus garryana</i> var. <i>breweri</i> .							4	15	6			

lus rostrata var. *californica* A. DC. and *Acer circinatum*, are most numerous (Table 3). These species and others form a small-tree stratum which is dense (averaging around 1400 stems over 1 cm dbh per ha), physiognomically mixed (including needle-leaved evergreen, broad-leaved evergreen, and broad-leaved deciduous species, the last predominant) and floristically rich (with 10 or more small-tree species in some stands).

TABLE 10. Distributions (frequencies) of shrubs and seedlings in a moisture-gradient transect for low elevations on serpentine in the central Siskiyou Mountains. For basis of data see heading of Table 4.

Transect step	Sites										Xeric Transect Constancy	Total Density
	1	2	3	4	5	6	7	8	9	10		
Conifer seedlings												
<i>Chamaecyparis lawsoniana</i> .	6										8	7
<i>Pinus monticola</i> .	5	15	28	14	6	15	2				44	98
<i>Pseudotsuga menziesii</i> .	2	14	15	10	11	6	3				46	71
<i>Libocedrus decurrens</i> .	1	2	10	8	3	14	11				52	
<i>Pinus lambertiana</i> .	1	1	2	6							12	12
<i>Pinus jeffreyi</i> .	2	1	3	2	2	4	1	1	1	1	24	16
<i>Pinus contorta</i> var. <i>murrayana</i> .								3			2	4
<i>Pinus attenuata</i> .									1		2	1
Shrubs												
<i>Rosa californica</i> C. & S.	1										2	2
<i>Physocarpus capitatus</i> .	2										2	2
<i>Salix</i> sp.	1										2	1
<i>Rhododendron occidentale</i> .	43								2		12	77
<i>Lithocarpus densiflora</i> var. <i>echinoides</i> .	5	29	34	24	30	10					44	317
<i>Umbellularia californica</i> .	3	2	10	8	8	6	1	1			40	44
<i>Vaccinium parvifolium</i> .	6	22	13	10	8	2	2	1			34	245
<i>Amelanchier alnifolia</i> .	1	4	10	19	3	7	2	2			38	72
<i>Rosa gymnocarpa</i> .	2	12	15	4	6	2	1	2			36	66
<i>Berberis pumila</i> .	2	25	8	14	8	18	9	6			44	211
<i>Garrya buxifolia</i> .	7	8	26	12	6	15	16	10			48	154
<i>Quercus chrysolepis</i> var. <i>vaccinifolia</i> .	13	54	47	46	27	38	22	15			76	646
<i>Arctostaphylos nevadensis</i> .	4	6	2	10	10	10	5	3	2		28	205
<i>Convolvulus polymorphus</i> .	6	x	9	5	4	14	10	16	9	2	62	116
<i>Rhamnus californica</i> var. <i>occidentalis</i> .	14	4	12	18	18	4	8	2	4	4	50	110
<i>Arctostaphylos cinerea</i> and <i>caneae</i> .	1	2	2	2	x		1				12	14
<i>Arctostaphylos viscida</i> .	3	6	4	14	6	10	7	3	6	50	82	
<i>Holodiscus dumosus</i> .	1	1	3				1				10	8
<i>Juniperus communis</i> .	x	1									2	1
<i>Juniperus sibirica</i> .	1	10	3	7	9	7					16	99
<i>Rubus vitifolius</i> .	6										2	15
<i>Castanopsis chrysophylla</i> var. <i>minor</i> .							4				2	7
<i>Rhododendron californicum</i> .							1				2	1
<i>Gaultheria shallon</i> .						7	20				4	145
<i>Quercus garryana</i> var. <i>breweri</i> .						6		2	1		6	10
<i>Ceanothus cuneatus</i> .								3			2	10
<i>Rhus diversiloba</i> .									1		2	1
<i>Cercocarpus betuloides</i> .									1		2	2

The principal shrubs are the evergreen species *Gaultheria shallon* and *Berberis nervosa*; representation of minor species is indicated in Table 4. Shrub coverage ranges from less than 10% to more than 40%, depending mainly on the occurrence of dense patches of *Gaultheria* and *Berberis*; herb coverage is lower—5 to 20%. The largest part of the herb stratum is made up of species with broad extent into sites other than ravines (see Table 5), which predominate on slopes above the stream-side. The distinctive stream-side flora itself is not nearly so well developed as in the more open ravine stands on other soils; *Boykinia elata* is the principal riparian species (see Table 5 and distributional grouping 1, Part V).

The sclerophyllous small trees—*Lithocarpus densiflora*, *Quercus chrysolepis*, *Arbutus menziesii*, and *Castanopsis chrysophylla*—predominate in the lower

TABLE 11. Distributions (frequencies) of herbs in a moisture-gradient transect for low elevations on serpentine in the central Siskiyou Mountains. For basis of data see heading of Table 4.

Transect step	Sites										Xeric Transect Constancy Density	Total	Xeric Transect Constancy Density
	1	2	3	4	5	6	7	8	9	10			
<i>Cypripedium californicum</i>	3										6	2	
<i>Darlingtonia californica</i>	6										4	25	
<i>Rudbeckia californica</i>	23										10	67	
<i>Tofieldia glutinosa</i> spp.													
<i>occidentalis</i>	10										6	44	
<i>Castilleja miniata</i>	5										4	18	
<i>Lotus oblongifolius</i>	5										2	32	
<i>Habenaria sparsiflora</i>	1										2	2	
<i>Habenaria unalascensis</i>	1										2	1	
<i>Trillium rivale</i>	1										2	1	
<i>Lilium occidentale</i>	x										0	0	
<i>Galium multiflorum</i>	2										2	7	
<i>Adiantum pedatum</i> var.													
<i>aleuticum</i>	x										0	0	
<i>Frillula atropurpurea</i>	4										6	6	
<i>Helenium bigelovii</i>	40	x									10	208	
<i>Lonicera hispida</i>	2	1									6	2	
<i>Goodyeara decipiens</i>	x	2									4	5	
<i>Liquiticum apifolium</i>	10	7	4	7							14	38	
<i>Chimaphila umbellata</i> var.													
<i>occidentalis</i>	1	22	1	5	2						14	81	
<i>Lilium howellii</i>	2	1	2	3	1						14	8	
<i>Smilacina racemosa</i>	5	1	2	1	1						14	13	
<i>Antennaria suffruticosa</i>	3		6	1	3						10	50	
<i>Angelica arguta</i>	3	1	6	2	1	1					14	19	
<i>Vancouveria chrysanthemifolia</i>	2	5	31	5	5						22	171	
<i>Epilobium rigidum</i>	2		2	6	14						12	109	
<i>Dipsorhynchus hookeri</i>	8	16	11	6							26	84	
<i>Trientalis latifolia</i>	17	18	35	26	31	11	14	8			62	838	
<i>Pyrola dentata</i>	4	14	6	2	4	6	x	2			42	106	
<i>Artemisia spathulata</i> var.													
<i>eastwoodiae</i>	2	30	20	4	14	3	2	1			42	207	
<i>Whipplea modesta</i>	16	16	29	7	17	10	18	1			50	413	
<i>Lomatium howellii</i>	2	10	15	8	12	17	4	1			40	158	
<i>Xerophyllum tenax</i>	16	18	27	28	20	39	24	2	1		62	562	
<i>Galium ambiguum</i>	4	7	17	20	30	31	25	18	5		78	634	
<i>Polygonia californica</i>	1	1	1	1	6	x	3	1			22	26	
<i>Schoenolirion album</i>	16		2	10	3	1	7	16			32	115	
<i>Iris bracteata</i>	5	31	49	46	29	39	31	22	5	1	86	944	
<i>Phlox speciosa</i>	2	15	24	9	14	5	10	11	5	1	58	266	
<i>Chelanthes siliqueosa</i>	4		5	3	1	15	20	20	12	44	157		
<i>Viola lobata</i>	2	4	14	14	23	15	22	6	9	5	431		
<i>Ceanothus pumilus</i>	1	3	15	3	5	13	22	36	71	53	72	869	
<i>Lomatium triternatum</i> var.													
<i>macrocarpum</i>	1	6	6	6	4	8	20	26	26	4	62	204	
<i>Hieracium corynocephaloides</i> var.													
<i>nudicaule</i>	1	13	5	6	8	9	12	5	11	3	60	180	
<i>Apocynum pumilum</i>	2										2	4	
<i>Senecio bolanderi</i>	2										2	2	
<i>Hieracium albiflorum</i>	7										2	15	
<i>Allotropa virgata</i>	1										2	2	
<i>Chimaphila menziesii</i>	x	1									2	2	
<i>Arenaria macrophylla</i>	1		1								4	6	
<i>Polyistachum munatum</i> var.													
<i>imbricans</i>	2	2	1								10	4	
<i>Linnæa borealis</i>	14			4							6	89	
<i>Silene campanulata</i> var.													
<i>orbiculata</i>	1		2								4	6	
<i>Campnula prenanthoides</i>	2		2								4	17	
<i>Artemisia parviflora</i> var.													
<i>pariflora</i>	2	4	2	4	4						14	38	
<i>Aster brickeioides</i>	6	7	10	26	2	3	x				34	104	
<i>Lotus crassifolius</i>	1	2				1	x				6	4	
<i>Sedum laevigatum</i>	1	2	6	1	1	1	6				18	30	
<i>Balsamorhiza deltoidea</i>	6	8	11	18	8	38	13	4	x		40	186	
<i>Balsamorhiza deltoidea</i> x											4	39	
<i>Platylepis hybrida</i>											2	2	
<i>Balsamorhiza platylepis</i>	12	6	10	2	2	4	1				16	162	
<i>Dicentra oregana</i>	2										2	2	

Table 11 (Cont.)

Sites	Menic	Transect step										Xeric Transect Constancy Density
		1	2	3	4	5	6	7	8	9	10	
<i>Castilleja pruinosa</i>											4	9
<i>Tauschia glauca</i>											2	36
<i>Haplopappus racemosus</i> spp.											16	94
<i>congeus</i>											2	170
<i>Sanicula peckiana</i>											2	2
<i>Eriophyllum lanatum</i> var.											2	182
<i>achilleoides</i>											2	675
<i>Horkelia sericea</i>											2	1
<i>Brickellia greenei</i>											0	0
<i>Veratrum insolitum</i>											2	2
<i>Microseris leptosepala</i> (Nutt.)											2	6
_{Gray}											2	14
<i>Pteridium aquilinum</i> var.											4	24
_{pubescens}											4	24
<i>Lupinus latifolius</i> var.											8	14
_{columbianus}											8	14
<i>Thlaspi alpestre</i> L.											4	10
<i>Achillea lanulosa</i>											8	11
<i>Eriogonum nudum</i>											8	15
<i>Streptanthus howellii</i>											0	0
<i>Horkebia tridentata</i>											0	0
<i>Cordylanthus viscidus</i>											20	71
<i>Erigeron foliosus</i> var.											24	102
_{confusus}											24	102
<i>Zygadenus micranthus</i>											28	28
<i>Calochortus howellii</i>											2	30
<i>Grindelia maritima</i> (Greene)											2	1
_{Steyermark}											2	1
<i>Lithospermum californicum</i>											4	2
<i>Phlox diffusa</i>											2	3
<i>Eriogonum pendulum</i>											0	0
<i>Penstemon laetus</i> ssp.											2	20
_{roeselii}											2	374
<i>Monardella odoratissima</i> var.											1	2
_{glauca}											2	1
<i>Senecio fastigiatus</i>											6	26
<i>Perideria oregana</i>											3	28
<i>Ceratium arvense</i>											3	2
<i>Sidalcea malvaefolia</i> ssp.											2	12
_{elegans}											1	46
<i>Calochortus tolmiei</i>											1	32
<i>Lomatium macrocarpum</i>											15	26
<i>Phacelia dasypetala</i> var.											51	20
_{ophitidis}											2	17
<i>Arenaria howellii</i>											6	22
<i>Brodiaea hendersonii</i>											2	9
<i>Allium foliaceum</i>											3	4
<i>Eriogonum ternatum</i>											x	30
<i>Gilia capitata</i>											1	2
<i>Erigeron bloomeri</i> var.											5	2
_{nudatus}											2	8
<i>Epilobium panniculatum</i> var.											2	5
_{hammondi}											9	29
<i>Blepharipappus scaber</i>											0	0
<i>Polygonum spargulariaefolium</i>											x	0
<i>Monardella villosa</i> var.											x	0
_{subserata}											x	0

tree stratum in all stands but those of ravines, with average stem densities per hectare increasing from 1200-1400 in submesic to 1600-2500 in xeric sites. Four major shrub species—*Rosa gymnocarpa*, *Rubus vitifolius*, *Berberis nervosa*, and *Rhus diversiloba*—occur in submesic and subxeric stands. Shrub coverage in these stands varies between 10 and 40%, averaging about 30%; herb coverage ranges from 2 to 12%, averaging 6.7%. The herb stratum also is dominated by a group of species which occur along almost the whole length of the moisture gradient on

TABLE 12. Distributions of trees in relation to elevation on quartz diorite in the central Siskiyou Mountains. Based on 6 moisture-gradient transects of different elevation belts; transects nos. 1 to 9 each included 50 stand samples of 0.1 or 0.2 hectare each in 10 transect steps, transect no. 11 included 16, 0.1 or 0.2 hectare samples in 8 transect steps. Density values are numbers of stems over 1 cm dbh (i.e. from the 0.5-1.5 in class up) or, where indicated, 8 in (20 cm) or 15 in (37 cm) or over in areas of 5.0 hectare per transect. Constaney values are per cents of the 50 (or 16) samples, 0.1 hectare each, of the transect in which the species occurred as a tree of the 1-in or larger diameter class.

Transect no. Elevations in feet Elevations in meters	1 1500-2500 460-670		3 2500-3500 670-1070		5 3500-4500 1070-1370		7 4500-5500 1370-1680		9 5500-6300 1680-1920		11 6300-7000 1920-2140	
	Dens.	Cons.	Dens.	Cons.	Dens.	Cons.	Dens.	Cons.	Dens.	Cons.	Dens.	Cons.
Conifers												
<i>Chamaecyparis lawsoniana</i>	93	13	499	46	439	54	370	32				
15" and over	42		167		160		121					
<i>Taxus brevifolia</i>	215	16	185	26	10	12	54	12				
<i>Pinus ponderosa</i>	1	2					3	2				
<i>Pseudotsuga menziesii</i>	904	96	767	92	674	100	435	90	5	10		
15" and over	378		506		604		330		4			
<i>Libocedrus decurrens</i>	1	2	15	6	8	6	72	24	11	12		
15" and over			2		2		37		6			
<i>Abies concolor</i>	5	10	215	40	905	100	1602	100	1241	58		
15" and over			11		143		477		404			
<i>Pinus lambertiana</i>	35	42	20	22	7	12	29	8	1	2		
15" and over	14		13		7		9					
<i>Abies nobilis</i>					2	2	71	40	1260	92	2400	100
15" and over					1		22		421		693	
<i>Tsuga mertensiana</i>							2	2	796	54	1338	75
15" and over									205		368	
<i>Pinus monticola</i>									1	2	3	6
Sclerophylls												
<i>Lithocarpus densiflora</i>	4236	100	2007	76	54	6						
8" and over	109		66		1							
<i>Quercus chryssolepis</i>	1422	90	463	48	59	8						
8" and over	171		57									
<i>Arbutus menziesii</i>	856	82	341	56	72	16						
8" and over	135		142		23							
<i>Castanopsis chrysophylla</i>	470	82	712	62	339	50	13	6				
8" and over	18		103		24							
Deciduous trees												
<i>Fraxinus oregana</i>	4	2										
<i>Cornus nuttallii</i>	201	60	48	12								
<i>Quercus kelloggii</i>	22	18	11	8								
<i>Acer circinatum</i>	642	46	198	22	32	10						
<i>Acer macrophyllum</i>	61	24	32	24	17	4	15	8				
<i>Salix</i> sp.	29	24	2	4	1	2	4	4				
<i>Alnus rubra</i> and <i>A. rhombifolia</i>	34	10	23	12	4	2	3	2				
<i>Amelanchier florida</i>	25	10	1	2	33	8	3	2				
<i>Corylus rostrata</i> var. <i>californica</i>	497	56	246	38	109	12	78	30	4	2		
<i>Acer glabrum</i> var. <i>douglasii</i>					14	6	190	24	23	10		
<i>Sorbus americana</i>							5	4				
Arborescent shrubs												
<i>Rhus diversiloba</i>	2	2										
<i>Philadelphus lewisii</i>	8	6										
<i>Rhododendron occidentale</i>	8	2										
<i>Ceanothus integerrimus</i>	4	4	15	10								
<i>Vaccinium parvifolium</i>	3	2	1	2	1	2						
<i>Holodiscus discolor</i>	171	38	33	20	55	18	53	18	5	2		
<i>Rhododendron californicum</i>			290	24	318	18	164	10				
<i>Quercus sadleriana</i>			1	2	24	6	17	2				
<i>Cornus stolonifera</i>					3	2	1	2			x	0
<i>Lonicera conjugialis</i>							3	2				
<i>Ceanothus velutinus</i>							3	2				
<i>Prunus emarginata</i>									1	2		

TABLE 13. Distributions of shrubs and seedlings in relation to elevation on quartz diorite in the central Siskiyou Mountains. Based on 6 moisture-gradient transects for different elevation belts; transects nos. 1 to 9 each included 50 undergrowth samples of 25, 1-m² quadrats each in 10 transect steps, transect no. 11 included 16 samples of the same size in 8 transect steps. All values are per mille frequencies in transects (the number of 1-m² quadrats, among 1000 such quadrats, in which a species was observed, based on 1250, 1-m² quadrats in the ten steps of transects 1 to 9, 400, 1-m² quadrats in transect no. 11). Observed presence in one or more samples of the transect, outside the 25 m² samples, is indicated by "x."

Transect no.	1	3	5	7	9	11
Elevation in feet	1500- 2500	2500- 3500	3500- 4500	4500- 5500	5500- 6300	6300- 7000
Elevation in meters	460- 760	760- 1070	1070- 1370	1370- 1680	1680- 1920	1920- 2140
Conifer seedlings						
<i>Chamaecyparis lawsoniana</i> ...	2	13	7	9		
<i>Taxus brevifolia</i> ...	12	12	5	5		
<i>Pseudotsuga menziesii</i> ...	64	46	35	18		
<i>Pinus lambertiana</i> ...	7	4	2	1		
<i>Libocedrus decurrens</i> ...	2	11	1	4	2	
<i>Abies concolor</i> ...						
<i>Abies nobilis</i> ...				8	64	100
<i>Tsuga mertensiana</i> ...					18	22
Sclerophyll seedlings						
<i>Lithocarpus densiflora</i> ...	291	174	4			
<i>Arbutus menziesii</i> ...	2		1			
<i>Castanopsis chrysophylla</i> ...	31	43	13	1		
<i>Quercus chrysolepis</i> ...	130	47	3	x	1	
Deciduous tree seedlings						
<i>Cornus nuttallii</i> ...	2	1				
<i>Acer macrophyllum</i> ...	2		9			
<i>Acer circinatum</i> ...	18	10	4	1		
<i>Corylus cornuta</i> var. <i>californica</i> ...	36	14	5	2		
<i>Amelanchier alnifolia</i> ...	6	2	4	2	4	
<i>Acer glabrum</i> var. <i>douglasii</i> ...			1	2		
Shrubs						
<i>Rhododendron occidentale</i> ...	1					
<i>Symplocarpus hesperius</i> ...	32	6	1			
<i>Berberis pumila</i> ...	17	15	2			
<i>Gaultheria shallon</i> ...	132	263	77			
<i>Berberis nervosa</i> ...	197	261	455	180		
<i>Pachystima myrsinites</i> ...	6	9	13	1		
<i>Rhus diversiloba</i> ...	226	85		1		
<i>Holodiscus discolor</i> ...	11	2	11	16		
<i>Symplocarpus rivularis</i> ...	8	1	4	32	19	
<i>Vaccinium parvifolium</i> ...	14	48	22		1	
<i>Rubus vitifolius</i> ...	126	204	177	38	1	
<i>Rosa gymnocarpa</i> ...	273	199	102	126	24	
<i>Rubus parviflorus</i> ...	19	3	2	15	2	
<i>Ceanothus integerrimus</i> ...	x					
<i>Rhododendron californicum</i> ...	65	30	14			
<i>Rubus nivalis</i> ...	8	70	37			
<i>Quercus sadleriana</i> ...	21	22	8	18		
<i>Vaccinium membranaceum</i> ...	1	13	28	8	10	
<i>Ribes lacustre</i> ...	2					
<i>Ribes marshallii</i> ...		1	58	211	157	
<i>Ribes lobii</i> ...	x	2				
<i>Cornus stolonifera</i> ...		x				
<i>Lonicera conjugialis</i> ...		x	6	x		
<i>Ribes viscosissimum</i> ...		25	36	13		
<i>Sambucus racemosa</i> var. <i>californica</i> (Greene) Jeps...				2		

diorite (see distributional groupings 5 & 6, part V). Important grasses include *Festuca occidentalis* and *F. ovina*, *Agrostis harfordii*, *Bromus suksdorfii*, and *Trisetum canescens*. The herb stratum on diorite includes a group of non-green vascular plants—*Cephalaria*

TABLE 14. Distributions of herbs in relation to elevation on quartz diorite in the central Siskiyou Mountains. For basis of data see heading of Table 13.

Transect no.	1	3	5	7	9	11
Elevation in feet	1500- 2500	2500- 3500	3500- 4500	4500- 5500	5500- 6300	6300- 7000
Elevation in meters	460- 760	760- 1070	1070- 1370	1370- 1680	1680- 1920	1920- 2140
<i>Cynoglossum grande</i> ...	3					
<i>Claytonia perfoliata</i> ...	1					
<i>Epilobium minutum</i> ...	2					
<i>Satureja douglasii</i> ...	2					
<i>Lathyrus pauciflorus</i> ...	6		1			
<i>Cypripedium fasciculatum</i> ...	2		3			
<i>Boykinia elata</i> ...	2		12			
<i>Adiantum pedatum</i> var. <i>aleuticum</i> ...		4	3			
<i>Aralia californica</i> ...		4	1			
<i>Lonicera hispida</i> ...	83	14				
<i>Tauschia kelloggii</i> ...	51	23				
<i>Campanula pannanoides</i> ...	106	56	7			
<i>Matia matioviae</i> ...	22	7	3			
<i>Boschniakia hookeri</i> ...	2	2	2			
<i>Allotropa virgata</i> ...	1	2	1			
<i>Whipplea modesta</i> ...	140	35	212	21		
<i>Linnaea borealis</i> ...	179	128	96	30		
<i>Asarum caudatum</i> ...	1	1	8	17		
<i>Tolmiea menziesii</i> ...	x		5	2		
<i>Collomia heterophylla</i> ...	22	6	13	4		
<i>Psoralea phystodes</i> ...	28	1	1	12		
<i>Cephalanthera austinae</i> ...	x	x	1	2		
<i>Listera caerulea</i> ...	2	1	9	1		
<i>Anemone alstroemeri</i> ...	23	24	126	163	62	
<i>Achlys triphylla</i> ...	193	307	805	542	128	
<i>Trifolalis latifolia</i> ...	161	77	205	296	37	
<i>Pteridium aquilinum</i> var. <i>pubescens</i> ...	141	163	53	63	14	
<i>Viola sempervirens</i> ...	57	154	248	78	4	
<i>Apocynum pumilum</i> ...	102	66	58	68	45	
<i>Senecio bolanderi</i> ...	105	12	40	62	1	
<i>Tiarella unifoliata</i> ...	5	27	78	197	12	
<i>Galium triflorum</i> ...	34	45	165	190	64	
<i>Goodmania decipiens</i> ...	38	40	91	49	1	
<i>Adenocaulon bicolor</i> ...	34	79	289	268	14	
<i>Vancouveria hexandra</i> ...	23	11	140	311	50	
<i>Disporum hookeri</i> ...	48	79	152	307	7	
<i>Iris chrysophylla</i> ...	10	14	8	20	11	
<i>Coptis laciniata</i> ...	5	32	6		11	
<i>Asarum hartwegii</i> ...	18	14	17	58	6	
<i>Clintonia uniflora</i> ...	5	21	81	172	15	
<i>Habenaria unalascensis</i> ...	1			x	2	
<i>Smilacina racemosa</i> ...	47	14	11	21	51	22
<i>Polystichum munitum</i> ...	88	53	42	17	2	
<i>Trillium ovatum</i> ...	38	48	62	126	50	10
<i>Chimaphila menziesii</i> ...	7	42	46	56	66	38
<i>Chimaphila umbellata</i> var. <i>occidentalis</i> ...	96	160	258	92	12	2
<i>Pyrola picta</i> ...	5	4	8	16	55	47
<i>Hieracium albiflorum</i> ...	93	58	160	172	202	197
<i>Phlox diffusa</i> ...	67	70	181	352	146	65
<i>Campanula scouleri</i> ...	10	29	171	328	204	35
<i>Arenaria macrophylla</i> ...	2		48	183	268	234
<i>Corallorrhiza maculata</i> ...	x	9	5	13	5	7
<i>Fragaria vesca</i> var. <i>braceata</i> ...	6	11	59	102	70	45
<i>Osmorhiza chilensis</i> ...	4	4	110	284	219	82
<i>Equisetum hyemale</i> var. <i>californicum</i> ...			2			
<i>Heuchera micrantha</i> ...			1			
<i>Galium bifolium</i> ...			1			
<i>Pleuricospora fimbriolata</i> ...			1			
<i>Cornus canadensis</i> ...			2			
<i>Mitchella repens</i> ...			14	82		
<i>Listera cordata</i> ...			1	4		
<i>Pyrola elatior</i> ...			3	2		
<i>Gaultheria ovatifolia</i> ...			1	1		
<i>Crassula striata</i> ...			x	2	x	x
<i>Pyrola bracteata</i> ...			2	x	x	x

Table 14 (Cont.)

Transsect no.	1	3	5	7	9	11	
Elevation in feet	1500-	2500-	3500-	4500-	5500-	6300-	
	2500	3500	4500	5500	6300	7000	
Elevation in meters	460-	760-	1070-	1370-	1680-	1920-	
	760	1070	1370	1680	1920	2140	
<i>Osmorrhiza occidentalis</i>	2	1			x		
<i>Vicia californica</i>	1	32	121	30			
<i>Lathyrus polyphyllus</i>	5	74	126	24			
<i>Pyrola secunda</i>	1	25	63	122	112		
<i>Claytonia spathulata</i>	2	7	41	74	2		
<i>Smilacina stellata</i>	9	94	251	98	5		
<i>Prunella vulgaris</i>	1						
<i>Lilium columbianum</i>	2						
<i>Sarcodes sanguinea</i>	1						
<i>Tradescantia caroliniana</i> (Walt.) Vail.	8						
<i>Lotus oblongifolius</i>	1						
<i>Mitella caulescens</i>	14						
<i>Orobanche uniflora</i>	3						
<i>Ranunculus uncinatus</i> var. <i>parviflorus</i> (Tort.) Bens.	1	1					
<i>Claytonia sibirica</i> L.	x	5					
<i>Habenaria sparsiflora</i>	2	2					
<i>Streptopus amplexifolius</i>	x	1					
<i>Circae alpina</i> var. <i>paciifica</i>	22	46					
<i>Athyrium felix-femina</i>	12	9					
<i>Lewisia leana</i>	2		x				
<i>Actaea spicata</i>	2	135	58				
<i>Nemophila parviflora</i>	16	37	15				
<i>Rubus lasiococcus</i>	2	39	157	130			
<i>Dicentra formosa</i>	3	5	14	25			
<i>Viola glabella</i>	39	171	58				
<i>Claytonia parvifolia</i>	2	1	12	22			
<i>Veratrum insolitum</i>	1	3	5	13			
<i>Mitella diversifolia</i>	1	22	18	5			
<i>Corallorrhiza mertensiana</i>	x	1	6	2			
<i>Bogkinia major</i>	10						
<i>Heracleum lanatum</i>	4						
<i>Lidiera convallarioides</i>	1						
<i>Cardamine breweri</i>	2						
<i>Pterospora andromedea</i>	1						
<i>Pentstemon angustifolius</i>	x	4					
<i>Hackelia jessicae</i>	5	20					
<i>Monardella odoratissima</i>	2	14					
<i>Agastache urticifolia</i>	2	11					
<i>Aquilegia formosa</i>	1	9	7				
<i>Senecio triangularis</i>	23	43	22				
<i>Polygonum phytolaccacefolium</i>	4	2	5				
<i>Viola sheltonii</i>	2	20	13				
<i>Artemisia latifolia</i>	79	365	253				
<i>Phacelia magellanica</i>	15	42	22				
<i>Erigeron alpinus</i>	2	32	13				
<i>Valeriana sitchensis</i> ssp. <i>sitchensis</i>	42	265	308				
<i>Angelica arguta</i>	1	5	10				
<i>Hydrophyllum occidentale</i>	67	76	10				
<i>Mertensia bella</i>	2	26	7				
<i>Erythronium revolutum</i> and <i>E.</i> <i>grandiflorum</i>	1	3	7				
<i>Mitella breweri</i>	5	39	25				
<i>Pentstemon nemorosus</i>	2	128	254				
<i>Pedicularis racemosa</i>	9	90	200				
<i>Artemesia douglasiana</i>	3						
<i>Epilobium parvifolium</i>	6						
<i>Pentstemon tolmiei</i> Hook.	11						
<i>Cryptogramma crispa</i> var. <i>acrostichoides</i> (R. Br.) C. B. Clarke	1						
<i>Collomia parviflora</i>	2						
<i>Delphinium nelsonii</i>	7	2					
<i>Saxifraga ferruginea</i>	4	10					
<i>Pentstemon newberryi</i>	2	38					
<i>Castilleja miniata</i>	2	13					
<i>Orogenia fusiformis</i>	1	7					
<i>Epilobium hornemannii</i>	6	18					
<i>Viola praemorsa</i>	2	5					

Table 14 (Cont.)

Transsect no.	1	3	5	7	9	11
Elevation in feet	1500-	2500-	3500-	4500-	5500-	6300-
	2500	3500	4500	5500	6300	7000
Elevation in meters	460-	760-	1070-	1370-	1680-	1920-
	760	1070	1370	1680	1920	2140
<i>Sanicula nevadensis</i>					2	7
<i>Anemone quinquefolia</i>					1	2
<i>Erysimum capitatum</i>					1	7
<i>Sedum oregonense</i>					23	10
<i>Aster siskiyouensis</i>					86	242
<i>Ligusticum grayi</i>					26	42
<i>Lupinus albicaulis</i>					10	2
<i>Gayophytum nuttallii</i>						2
<i>Castilleja pruinosa</i>						2
<i>Eriophyllum lanatum</i>						2
<i>Epilobium angustifolium</i>						15
<i>Polygonum danisae</i>						25
<i>Calyptridium umbellatum</i>						
(Torr.) Greene						5
<i>Phacelia procera</i>						2

lanthera austinae, *Allotropa virgata*, *Corallorrhiza maculata* and *C. striata*, *Pyrola picta* f. *aphylla* (Smith) Camp, *Pleuricospora fimbriolata*, and *Boschniakia hookeri*—which are rare or absent on the other soils.

In xeric stands (Fig. 4) the coverage of *Pseudotsuga* (and the smaller numbers of *Pinus lambertiana*) is relatively low, generally well below 50%. In most stands *Lithocarpus* is most numerous among smaller stems, but *Arbutus* and *Q. chrysolepis* share dominance with it. *Rosa gymnocarpa* and *Rhus diversiloba* are the principal shrub species, as in subxeric sites; these and the prostrate *Rubus vitifolius* are often the only shrub species present, apart from tree seedlings. Shrub coverage averages around 30%, but with tree seedlings making up most of this. Herb coverage is consistently low (1-7%), with *Pteridium aquilinum* var. *pubescens* the major species of the herb stratum (see Table 5, distributional groups 6 and 8).

Stands which are floristically similar to these, but without large trees of *Pseudotsuga* or *P. lambertiana*, occur on some slopes, especially south-facing ones. These stands are considered products of more severe fires, and fire-effects are reflected both in size-distributions of the sclerophyll canopy and in the fact that *Pseudotsuga* is present as seedlings, but absent as a tree.

Some trends along the moisture gradient in low-elevation diorite vegetation have been commented on (Whittaker 1953:49, 1954b). Among the trees, the deciduous broad-leaf growth-form predominates in numbers of stems of all sizes in mesic sites and declines to 1-2% of stems in xeric sites. Character of the canopy changes from evergreen needle-leaf dominance in mesic sites, with relatively small numbers of sclerophylls, to a two-level canopy of *Pseudotsuga* and the sclerophylls in submesic and subxeric sites, to a closed canopy of sclerophylls with an overgrowth of large *Pseudotsuga* in xeric sites. Shrub coverage

TABLE 15. Distributions of grasses and grass-like plants in relation to elevation on quartz diorite (transects 1-11), and in relation to parent-materials at low elevations (transects 1 and 3 on diorite, 18 on olivine gabbro, 15 on serpentine). Observed presence in the samples of a transect is indicated by "x." Per mille frequencies, and densities of apparent individuals, for 1000, 1-m² quadrats are given for all grass, sedge, and rush species together, based on 400, 1-m² quadrats in transect 11, 1250 quadrats in other transects.

Transect no.	1	3	5	7	9	11	18	15
Elevation in feet	1500-2500	2500-3500	3500-4500	4500-5500	5500-6300	6300-1500	1500-2000	2000-
Elevation in meters	460-760	760-1070	1070-1370	1370-1680	1680-1920	1920-2240	2240-670	670-915
Parent material	diorite						gabbro	serpentine
<i>Festuca ovina</i>	x					x		x
<i>Festuca rubra</i>	x							
<i>Melica harfordii</i>	x	x					x	
<i>Luzula campestris</i>	x	x	x				x	x
<i>Triquetum canescens</i>	x	x	x	x			x	x
<i>Bromus suksdorfii</i>	x	x	x	x	x			
<i>Melica subulata</i>	x	x	x	x	x	x		
<i>Festuca occidentalis</i>	x	x	x	x	x	x	x	
<i>Festuca subulata</i>		x						
<i>Carex bolanderi</i>		x						
<i>Festuca subuliflora</i>	x	x	x					
<i>Bromus occidentalis</i>		x						
<i>Carex laevigulmis</i>	x	x						
<i>Carex mertensii</i>	x	x						
<i>Luzula parviflora</i>	x	x						
<i>Pleuropogon refractus</i>	x	x						
<i>Glyceria striata</i>		x						
<i>Luzula apicata</i>		x	x	x				
<i>Carex tracyi</i>			x	x				
<i>Carex rossii</i>				x	x			
<i>Triquetum spicatum</i>				x	x			
<i>Poa bolanderi</i>			x	x				
<i>Juncus parryi</i>					x			
<i>Poa nervosa</i>					x			
<i>Elymus glaucus</i>		x	x		x			
<i>Bromus carinatus</i>				x	x			
<i>Juncus ensifolius</i>				x				
<i>Festuca californica</i>				x				
<i>Carex multiculus</i>				x				
<i>Eriophorum crinigerum</i>				x	x			
<i>Carex debiliformis</i>				x	x			
<i>Agrostis hallii</i>				x	x			
<i>Sisyrinchium</i>				x	x			
<i>Carex angustior</i>				x				
<i>Calamagrostis kuhneoides</i>				x				
<i>Poa rhizomata</i>				x	x			
<i>Melica geyeri</i>				x				
<i>Bromus breviaristatus</i>				x				
<i>Dianthonia californica</i>				x				
<i>Koeleria cristata</i>				x				
<i>Sitanion jubatum</i>				x				
All graminoid species								
Frequency/1000 m ²	110	96	269	307	304	227	182	728
Density/1000 m ²	269	211	731	789	845	490	451	6066

is moderate, averaging 20-35% throughout the transect; herb coverage is low, declining from an average of 12% in mesic to 6% in xeric sites. The whole vegetation pattern, dominated as it is by larger evergreen needle-leaved and smaller evergreen sclerophyll trees, may be described as Mixed Evergreen Forest (Munz & Keck 1949); but the gradual changes along the moisture gradient make mesic and xeric stands very unlike one another. Within this vegetational



FIG. 4. View within a sclerophyll-Pseudotsuga forest on diorite on an open SE slope, inclination 30°, at 670 m, Oregon Caves area, Siskiyou Mts., Ore. *Pseudotsuga menziesii*, *Quercus chrysolepis*, and few *Lithocarpus densiflora*; *Rhus diversiloba*, *Rosa gymnocarpa*, *Lonicera hispida*, *Polystichum munitum*, *Hieracium albiflorum*, *Whipplea modesta*. July 19, 1950.

continuum, three community-types are distinguished—Chamaecyparis-Pseudotsuga forest with few sclerophylls and many deciduous stems in mesic sites, Pseudotsuga-sclerophyll stands with two-level canopies in intermediate sites, and sclerophyll-Pseudotsuga stands with quite open growth of conifers in xeric sites.

LOW ELEVATIONS ON GABBRO

The general description of the diorite vegetation as "mixed evergreen forest" can apply also to the gabbro vegetation pattern at low elevations. Apart from over-all physiognomic similarity and the sharing of some species, however, the two vegetation patterns are quite different. The gabbro vegetation is much more open than that on diorite (cf. Figs. 4 and 5). Average densities of large stems of conifers (37 cm dbh and over) were less than half as great on gabbro (8.4 stems/ha vs. 20.5 on diorite); and density of larger sclerophyll stems is much lower on gabbro in more xeric sites. It is consequently possible to stand on one hillside in the gabbro area and look through the canopy to the soil on another, nearby hillside (Fig. 6); in the diorite area one cannot similarly look through the dense evergreen canopies. The under-growth strata on gabbro are in general of lower cover-



FIG. 5. View within a more open *Pinus*-*Pseudotsuga*-sclerophyll forest on gabbro, on an open east slope, inclination 35°, at 370 m near Panther Creek, Siskiyou Mts., Ore. *Pinus lambertiana*, *Arbutus menziesii*, *Quercus chryssolepis*, *Rhus diversiloba*, *Polygala californica*, *Whipplea modesta*, *Chimaphila umbellata* var. *occidentalis*. July 15, 1951.

age than on diorite, and of quite different floristic composition.

Stands of ravines in the gabbro area are dominated by *Pseudotsuga menziesii* and *Chamaecyparis lawsoniana*; but significant numbers of *Pinus lambertiana*, *P. ponderosa*, and *Libocedrus decurrens* also occur. Below the quite open canopy is an open stratum of sclerophylls; deciduous tree species are much less numerous on gabbro than on diorite (Table 6). Shrub coverage in ravines is patch-like and variable, but generally low; *Rhododendron occidentale* is the principal species. The stream-side herb flora is much richer in species than on diorite (Table 8). Like the rest of the gabbro flora, it includes some species which are shared with the diorite flora, some shared with the serpentine flora (see distributional group 1, Part V), and some (*Luina hypoleuca*, *Peltiphyllum peltatum*, *Epipactis gigantea*, *Erigeron cervinus*) encountered only in the gabbro transect. A number of sedges and rushes are conspicuous in the herb stratum of ravines on gabbro and serpentine (see distributional group 1).

On mesic and submesic slopes, the stands are dominated by *Pseudotsuga* and *P. lambertiana*, in a quite open tree stratum, together with a denser, but not closed, lower stratum of sclerophylls. Estimated coverages for the two strata averaged 40% for the



FIG. 6. View into a *Pinus*-*Pseudotsuga*-*Quercus* stand on gabbro from across a ravine; the stand photographed is on a NW slope, 32° inclination, 400 m, York Creek, Siskiyou Mts., Ore. *Pinus lambertiana*, *Pseudotsuga menziesii*, *Quercus chryssolepis*, *Lithocarpus densiflora*, *Umbellularia californica*. *Kalmiopsis leachiana* occurs in this stand and on ridge above. July 8, 1950.

conifers, 80% for the sclerophylls. The relative importance of *P. lambertiana* is much greater than on diorite; the ratio of larger stems of *P. lambertiana* to *Pseudotsuga* was about 2:3 on the average on gabbro and only 1:20 on diorite. Three of the major sclerophylls—*Lithocarpus densiflora*, *Quercus chryssolepis*, and *Arbutus menziesii*—are shared with the diorite vegetation; but the sclerophyll stratum on gabbro includes two major species, *Umbellularia californica* and *Arctostaphylos cinerea* Howell, which are essentially absent from the diorite vegetation.

The principal shrub species on gabbro are *Rhus diversiloba*—the usual shrub dominant—and *Rhamnus californica* var. *occidentalis* and *Vaccinium ovatum*, both of which are rare or absent on diorite. Shrub coverage increased from averages of 10-12% in submesic sites to 20-32% in xeric ones; herb coverage was low, averaging between 2% and 7% throughout the transect. The rare endemic shrub *Kalmiopsis leachiana* occurs in some, more xeric stands. Grasses

of broad distribution in the gabbro transect include *Melica harfordii*, *Festuca occidentalis*, *F. californica*, and *Trisetum canescens*, together with the rush *Luzula campestris*.

In most xeric stands on gabbro (transect steps 7-10) *Pseudotsuga* is strongly outnumbered by pines (*P. lambertiana* and *P. ponderosa*). These stands are unlike the *Pseudotsuga*-dominated forests on diorite, and like the serpentine vegetation, in the mixture of pines with *Pseudotsuga* and *Libocedrus* in the upper tree stratum and in the low coverage of this stratum (below 50% and in some stands below 20%). The xeric stands on gabbro differ also from those on diorite in the occurrence of *Arctostaphylos cinerea* as the most numerous small tree and in the low coverage of the sclerophyll stratum (10 to 40%).

The gabbro vegetation is thus in general more open, less strongly dominated by *Pseudotsuga*, with greater importance of pines and smaller of deciduous trees, than that on diorite. *Libocedrus* and *P. ponderosa* are absent from low-elevation diorite in this area, except as rare large individuals presumably surviving from past disturbance. On gabbro they are present along most of the moisture gradient, with all size classes including current reproduction represented; presumably the more open structure of gabbro vegetation makes possible their reproduction there. Physiognomic trends along the moisture gradient are less striking on gabbro than on diorite. Coverage of conifers declines somewhat, and proportion of pines among them increases, along the gradient from mesic to xeric. Sclerophyll coverage declines along the gradient from submesic to xeric; but sclerophyll stem numbers increase toward more xeric sites because of the larger numbers of small stems of *Arctostaphylos*.

LOW-ELEVATIONS ON SERPENTINE AND THE TWO-PHASE EFFECT

The vegetation of serpentine is still more open than that of gabbro (Fig. 7); even in mesic sites the



FIG. 7. A serpentine landscape at low elevations in the Siskiyou Mts., Ore.; view of Eight-Dollar Mountain, west-facing slopes, from Oak Flat Road, July 9, 1950. Open *Pinus jeffreyi* woodlands occur on the most open W- and SW-facing slopes, mixed conifers with patchy or 2-phase shrub undergrowth in somewhat less xeric situations, and denser (but still rather open) stands of *Chamaecyparis lawsoniana*, *Pinus monticola*, and *Pseudotsuga menziesii* on most mesic slopes and in ravines.

low-elevation serpentine stands have a characteristic sparse and xerophytic appearance. In the tree stratum, pines are more numerous than *Pseudotsuga* and other conifers, and deciduous broad-leaved trees are absent. The sclerophyllous trees are also virtually absent, as trees, from serpentine. Some of these sclerophylls are very much in evidence on serpentine, however, as shrubs. *Quercus chrysolepis* is represented on serpentine by var. *vaccinifolia* (Kell.) Engelm., the most abundant single shrub species there; *Lithocarpus densiflora* is represented by var. *echinoides*, *Umbellularia californica* by an unnamed shrubby variant, and *Castanopsis chrysophylla* by var. *minor* (uncommon in the study area). *Quercus garryana* occurs on serpentine as the shrubby var. *breweri* (Engelm.) Jeps. Among other trees and shrubs a series of congeneric pairs appear in non-serpentine and serpentine floras, with the serpentine species in each case of smaller stature: *Amelanchier floridana* and *A. gracilis* Heller, *Garrya fremontii* and *G. buxifolia*, *Rhamnus purshiana* and *R. californica* var. *occidentalis*, *Holodiscus discolor* and *H. dumosus* (Nutt.) Heller, *Ceanothus integerrimus* and *C. pumilus*, *Berberis nervosa* and *B. pumila*. The impression given by the serpentine vegetation is that, as the physiognomic changes evident from diorite to gabbro vegetation are carried a step further onto serpentine, the coniferous tree stratum is reduced to an open stand mostly of smaller pines, the sclerophyllous tree stratum shrunken to a shrub layer, and the other broad-leaved trees and shrubs replaced by smaller shrubs and dwarf shrubs.

Stands of ravines on serpentine (Whittaker 1954b: Fig. 2) are still more open than those on gabbro, with *Chamaecyparis lawsoniana* and *Pinus monticola* each contributing about $\frac{3}{8}$ of the coniferous stems (Table 8). *P. monticola*, however, is a small tree on serpentine, and among larger stems *Chamaecyparis* is strongly dominant. As on gabbro, there are numerous small stems of *Rhododendron occidentale* along the streams; and most other shrubs of the serpentine flora may occur in ravines at low coverages. In the herb stratum the distinctive character of the serpentine flora is apparent; rare and narrowly endemic species (*Cypripedium californicum*, *Rudbeckia californica*, *Darlingtonia californica*, *Trillium rivale*, *Lilium howellii* and *L. occidentale*) are mixed with more widespread species of bogs and other moist situations (see Table 11, distributional groups 1 and 4).

Tree strata on submesic and subxeric sites are typically mixtures of several conifers—*Libocedrus*, *Pseudotsuga*, *Pinus jeffreyi*, *P. monticola*, *P. lambertiana*, and in some stands *P. attenuata*. Tree coverage of these stands is low, generally below 50%, but shrub coverage is high, often over 80% in submesic stands, giving these a most distinctive physiognomy of small conifers in open growth above a dense, low sclerophyllous shrub stratum (Fig. 8). Shrub coverages increase along the moisture gradient from 20-50% in ravines to 50-90% in submesic stands,



FIG. 8. A stand of a mesic slope on serpentine at low elevations; SE-facing slope above Cedar Creek, near the Wimer Road, at 650 m, Siskiyou Mts., Ore. An open stand of *Chamaecyparis lawsoniana*, *Pinus monticola* and *Pseudotsuga menziesii* above a dense evergreen shrub layer, 90% coverage, dominated by *Lithocarpus densiflora* var. *echinoides* and *Quercus chrysolepis* var. *vaccinifolia*. October 10, 1951.

and then decrease to 20-50% in subxeric and 0-20% in xeric stands. *Quercus chrysolepis* var. *vaccinifolia*, *Lithocarpus densiflora* var. *echinoides*, *Vaccinium parvifolium*, *Garrya buxifolia*, and *Umbellularia californica* are the principal species and form the canopy of shrubs of middle height—generally below, but approaching 1 m, with *Umbellularia* extending somewhat higher.

Herb coverages in submesic sites on serpentine were relatively low, ranging from 1 to 20% and averaging 11%, but increased along the moisture gradient to 10-40%, averaging 30%, in subxeric sites. Composition of the floristically rich herb stratum may be judged from Table 11. Grasses and grass-like plants included *Poa rhizomata*, *Trisetum canescens*, *Melica geyeri*, *Luzula campestris*, *Calamagrostis koe-*

leroides, and an abundant but undetermined small *Carex* sp.

In most stands of intermediate sites on serpentine, the shrubs show a patch-wise distribution, giving undergrowth of these stands a two-phase character of essentially closed shrub cover alternating with shrub-less openings with grasses and other herbs (Whittaker 1954b). Since shrub cover is high in submesic sites but declines toward more xeric ones, there is a reversal of phase along the moisture gradient. In submesic stands the shrubs form the continuous phase with discontinuous openings (Whittaker 1954b: Fig. 3); but as shrub cover falls below 50% in subxeric sites, the grassy openings form the continuous phase with discontinuous shrub patches (Fig. 9). Diameters of patches of the discontinuous phase in the samples were mostly 2-5 m, with occasional larger or smaller ones.

In such two-phase vegetation the distributions of shrub populations are necessarily non-random; but the tendency toward correlation with one of the phases applies to populations other than those of the dominant shrubs. Ten samples from vegetation of two-



FIG. 9. A mixed-conifer stand with 2-phase undergrowth on serpentine, open ENE slope, 25° inclination, 740 m, on Tennessee Mtn. in the Siskiyou Mts., Ore. *Pinus jeffreyi*, *P. monticola*, *P. lambertiana*, *Libocedrus decurrens*, *Pseudotsuga menziesii*, in open stand (about 40% coverage), scattered shrub patches (24% coverage) dominated by *Quercus chrysolepis* var. *vaccinifolia*, and sparse grass (29% coverage). July 18, 1950.

phase character were selected, evenly divided between submesic and subxeric stands and numbers of herb and shrub quadrats; and plant populations were tabulated by their occurrence in quadrats assigned, by their predominant character, to either the shrub or herb phase. Table 16 summarizes results for species

TABLE 16. Two-phase relations of species populations in serpentine vegetation of the central Siskiyou Mountains.

	CONSTANCY	DENSITY	FREQUENCY		FREQUENCY RATIO	
			No. out of 125 1-m ² quadrats in which observed			
			(10 samples)	open	shrub	open/shrub
Shrubs						
<i>Quercus chrysolepis</i> var. <i>vaccinifolia</i>	10	20	186	16	85	0.19
<i>Umbellularia californica</i>	5	4	8	2	8	0.25
<i>Garrya buxifolia</i>	6	9	34	7	22	0.32
<i>Amelanchier gracilis</i>	5	5	12	4	10	0.40
<i>Lithocarpus densiflora</i> var. <i>echinoides</i>	4	12	31	9	17	0.53
<i>Vaccinium parvifolium</i>	3	27	47	7	12	0.58
<i>Arcostaphylos viscida</i>	5	12	13	10	11	0.9
<i>Rhamnus californica</i> var. <i>occidentalis</i>	5	14	13	12	11	1.1
<i>Rosa gymnocarpa</i>	5	16	8	10	7	1.4
<i>Berberis pumila</i>	6	39	27	17	12	1.4
<i>Arcostaphylos nevadensis</i>	3	25	11	10	5	2.0
<i>Convolvulus polymorphus</i>	6	19	4	14	4	3.5
Herbs						
<i>Whipplea modesta</i>	8	48	131	15	34	0.44
<i>Trentalis latifolia</i>	8	67	98	13	24	0.54
<i>Xerophyllum tenax</i>	6	53	36	18	22	0.82
<i>Phlox speciosa</i>	7	22	34	14	12	1.2
<i>Iris bracteata</i>	10	159	157	48	47	1.0
<i>Viola lobata</i>	5	73	45	17	17	1.0
<i>Aster brickelliioides</i>	4	22	14	8	7	1.1
<i>Lomatium nudicaule</i>	4	10	8	7	6	1.2
<i>Balsamorhiza deltoidea</i>	6	46	32	24	19	1.3
<i>Galium ambiguum</i>	10	122	62	29	18	1.6
<i>Ceanothus pumilus</i>	6	110	33	27	13	2.1
<i>Lomatium nudicaule</i>	6	39	11	15	6	2.5
<i>Hieracium cilioglossoides</i> var. <i>nudicaule</i>	6	22	8	12	4	3.0
<i>Eriogonum foliosum</i> var. <i>confinum</i>	4	34	9	6	2	3.0
<i>Carex sp.</i>	4	117	28	19	6	3.2
<i>Horkelia sericata</i>	2	72	9	12	3	4.0
<i>Eriophyllum lanatum</i> var. <i>achilleoides</i>	2	8	1	4	1	4.0
<i>Polygonia californica</i>	4	8	1	6	1	6.0
<i>Senecio fastigiatus</i>	2	16	1	7	1	7.0
<i>Cheilanthes silvosa</i>	5	10	1	9	1	9.0
<i>Cordylinea viscida</i>	4	20	0	9	0	
<i>Zygadenus micranthus</i>	4	12	0	7	0	
<i>Perideridia oregana</i>	2	4	0	3	0	

represented by significant numbers in 125 quadrats of each phase. Of the shrub species, the first six are necessarily concentrated in the shrub phase, for they form the shrub canopy of this phase. Of the other species one (*Rosa gymnocarpa*) is often part of the shrub canopy but occurs also in the openings;

Arctostaphylos viscida is taller, and *Berberis pumila*, *Arctostaphylos nevadensis*, and *Convolvulus polymorphus* are lower than the shrub canopy, and occur independently of it.

Relations of herb species to the phases are significantly correlated with their moisture-gradient relations. *Whipplea* and *Trentalis*, the only species concentrated in the shrub phase, are the only species whose distributional centers are in mesic or mesies-mesic sites; and they are also the only herb species listed which occur in the well-shaded herb stratum on diorite. The next 8 species listed, *Xerophyllum* to *Galium ambiguum* are centered in submesic, or submesic and subxeric, sites; the last 13 species are centered in subxeric or xeric sites. In general, the more a species population is concentrated toward the mesic end of the gradient, the more it is concentrated also in the shrub phase; the more a species is concentrated toward more xeric sites, the more it is concentrated in the open phase. Grasses in general show marked concentration in the open phase, but significant data are not available for individual species. Such data suggest different responses of species populations to the somewhat different microclimatic and soil conditions underneath the shrubs and in the grassy openings. It appears that these micro-environments may also influence tree distributions through effects on seedlings. *Pseudotsuga*, *P. monticola*, and *P. attenuata* tended to be concentrated in the shrubs; *Libocedrus* to be indifferent or less strongly concentrated in the shrubs; *P. jeffreyi* to be concentrated in the open.

The two-phase character is developed in quite different degrees in different stands. The condition is most easily recognized in those stands in which the proportions of shrub cover and opening are relatively even. Comparison of samples with regard to disturbance and succession suggests that the two-phase effect is characteristic of climax, rather than successional, stands. The two-phase effect seems best developed in some stands with well-developed soil, but poorly developed in stands with more rocky, clearly immature soils. It seems best developed also in those stands least disturbed by fire, but poorly developed in stands with more severe fire effects.

Two-phase vegetation, with reversal of phase along an environmental gradient, is known for other circumstances—as the break-up of taiga and krummholz into tundra in the far North (Rousseau 1952), the transition of deciduous chaparral into semi-desert in the Wasatch Mountains (Hayward 1948), and the aspen groveland (Coupland & Brayshaw 1953, Lynch 1955). In these circumstances the two-phase character seems transitional, an "ecotone" of the "mosiac-insular" type considered by Nyzenko (1948) the most common kind of ecotone. In a broad sense, the two-phase vegetation of the Siskiyou serpentine is a transition between closed forests of high elevations and the open pine steppes of low elevations and most xeric sites (Fig. 12). The two-phase vegetation is an extensive community-type, diverse within

itself, however, with a distinctive physiognomy, and many character-species which are centered within it rather than in forest or pine steppe. Species populations show all degrees of correlation with one or another of the phases; the phases are by no means distinct and relatively immiscible communities in mosaic arrangement.

Too facile a description of this vegetation as "an ecotone between two communities" may do more to obscure than clarify its significance, for the meanings of "ecotone" and "community" in this description are scarcely understood by ecologists. The author would prefer a different descriptive interpretation. The open tree stratum on serpentine makes possible well-developed undergrowth communities of high coverage. Along the whole of the moisture gradient the undergrowth is of mixed shrubs, and grasses and other herbs; but the shrub populations are concentrated in submesic sites, the grasses in more xeric ones. Along the moisture gradient from submesic to xeric sites, there is gradual shift of balance between these two major components of the undergrowth, as the extent of the woody strata which the sites can support declines. Since there is also a tendency for the shrubs to grow in closed patches, the vegetation assumes a two-phase character with the relative importance of the phases shifting continuously along the moisture gradient.

In stands of xeric sites shrub coverage ranges downward to zero. Undergrowth of these stands is predominantly of grasses, in rather sparse growth; grass-like plants include *Stipa lemmoni*, *Sitanion jubatum*, *Melica geyeri*, *Elymus glaucus*, *Festuca ovina*, *Bromus breviristatus*, *Danthonia californica*, *Agrostis hallii*, *Koeleria cristata*, *Carex* sp., and *Luzula campestris*. With these occur many broad-leaved herb species (Table 11, distributional groupings 7 and 9). In some xeric stands *P. jeffreyi* is the only tree species present, in very open stand (Fig. 10). *Libocedrus* occurs in smaller numbers in



FIG. 10. Jeffrey pine woodlands with widely scattered *Arctostaphylos viscida* and grassy floor, on dry flats and lower slopes on serpentine. Oak Flat Road, about 400 m, Siskiyou Mts., Ore., October 9, 1951.

most, and *Pseudotsuga* in some stands. *Arctostaphylos viscida* forms a very open high-shrub stratum in some stands. Physiognomically these stands, with their pines in scattered growth above a

grassy floor, are unlike anything yet described; they are of the widespread physiognomic type which may be termed pine steppe or pine woodland.

Although pine woodlands are of very wide occurrence, the two-phase stands of intermediate sites on Siskiyou serpentine are most distinctive. Their physiognomy—mixed conifers in open growth above a dense scrub-oak stratum with grassy openings—is scarcely duplicated elsewhere to the author's knowledge, although pine heath and mixed conifers with heath or chaparral are reported from serpentine in other areas (Ritter-Sudnicka 1953, Yamanaka 1954, 1956, 1957, McMillan 1956). Neither physiognomic type occurs on diorite or gabbro in the study area. Comparing the three vegetation patterns described here, there is progressive reduction of tree-stratum coverage and biomass from diorite through gabbro to serpentine; while undergrowth strata are better developed on serpentine. Compared with the other vegetations, the serpentine vegetation suggests a shift of the concentration of plant life from the tree stratum downward toward the shrub and herb strata (Whittaker 1954b). Viewing serpentine vegetation as a whole, a comparable shift of vegetational biomass toward the lower strata along the moisture gradient is suggested—from the trees in most mesic sites to a highly developed shrub stratum in intermediate and herb stratum in xeric sites. Within the serpentine vegetation the herb and shrub strata show a distinct inverse correlation, such as is encountered in some vegetation conditions (Whittaker 1956) but not in others, and not on the other soils in the Siskiyous.

Within the Siskiyou Mountains at low elevations, serpentine vegetation shows a general consistency with what has been described; but climatic variation, the extreme localization of some of the species, and probable variation in chemistry of serpentine rocks imply differences in floras from one outcrop to another. Smaller outcrops of serpentine, such as may be observed west and northwest from the diorite study area, often support vegetation and floras which are intermediate to those of serpentine and more typical soils. Extent of development of the serpentine flora on one of these outcrops seems in general to be directly proportional to its size and inversely proportional to its distance from one of the larger serpentine areas. Departing also from what has been described are the dense stands of young stems of *Pinus attenuata* encountered in many areas, and the Jeffrey pine woodlands on private land near the valleys, with shrub strata dominated by *Ceanothus cuneatus*. These conditions are thought to be products of disturbance, the former by fire and the latter by grazing.

FOREST VEGETATION OF HIGHER ELEVATIONS ON DIORITE

Although intensive study was concentrated in a single area, serpentine vegetation was observed at all elevations in other areas of the Siskiyou Mountains.

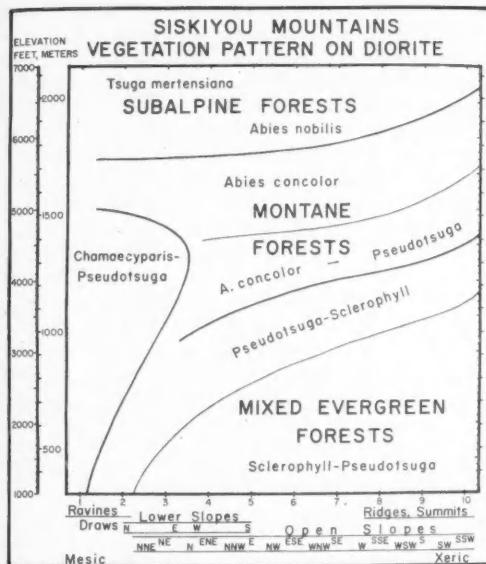


FIG. 11. Mosaic chart of vegetation on quartz diorite, central Siskiyou Mountains, Oregon.

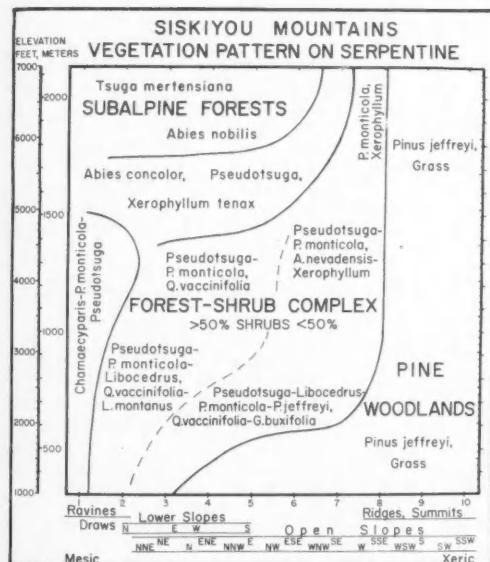


FIG. 12. Mosaic chart of vegetation on peridotite and serpentine, central Siskiyou Mountains, Oregon (*L. montanus* = *Lithocarpus densiflora* var. *echinoides*).

The diorite vegetation was intensively sampled at all elevations in the principal study area. Figs. 11 and 12 present "mosaic charts" (Whittaker 1956) for the two patterns in the central Siskiyous, based on 270 vegetation samples on diorite, 70 vegetation samples and 90 other field records of serpentine stands.

In the diorite pattern the sclerophylls are concentrated in the low-elevation, xeric sites, the lower right corner of Fig. 11. With increasing departure from these sites, toward either more mesic situations or higher elevations, the proportion of sclerophylls in the stands decreases. This distributional relation, and the complex relations of moisture conditions to both topography and elevation, imply an oblique boundary for the sclerophyll-Pseudotsuga type. Beyond this boundary the Pseudotsuga stands form a transition to Chamaecyparis-Pseudotsuga stands at lower and *Pseudotsuga-Abies concolor* stands at higher elevations.

The Chamaecyparis-Pseudotsuga forests, which are rather narrowly restricted to ravines and most mesic slopes at lower elevations, expand toward higher elevations onto many sheltered slopes and some open northerly ones. The character of these forests changes gradually as they are followed from the low elevations already described to elevations above 1200 m. Representation of the sclerophylls and all other broad-leaved trees decreases toward higher elevations, while *Abies concolor* becomes increasingly important. Shrub coverage is low; the low-elevation species *Rosa gymnocarpa*, *Berberis nervosa*, and *Rubus vitifolius* are joined by other species largely restricted to forests of higher elevations—*Quercus sadleriana*, *Ribes marshallii*, *Vaccinium membranaceum*. The change in the herb stratum toward higher elevations is more conspicuous; for herb coverage increases to 20-60%, with many mesophytic species including most of these of low-elevation mesic stands and montane forests (distributional groups 3, 6, 10, and 11).

At elevations between 1200 and 1850 m (4000-6000 ft) "Montane Forests" occur, dominated by Pseudotsuga and *Abies concolor* at lower, by *A. concolor* at higher, elevations. Chamaecyparis is present in some stands of more mesic situations, *Libocedrus decurrens* in some stands of more xeric situations. The only broad-leaved trees of significance are *Acer glabrum* var. *douglasii* and *Corylus rostrata* var. *californica*; sclerophylls are wholly absent above lower elevations of the montane forests. Shrub coverage is low, generally 0-10%, with *Rosa gymnocarpa*, *Berberis nervosa*, *Rubus vitifolius*, and *Holodiscus discolor* the principal species. The herb stratum is floristically rich and of high, though variable coverage—30-80% in most stands, but as high as 90% and, below 10% in some stands. These forests show, in less marked degree, the gradation from rich to poor herb strata to be described for the subalpine forests. Herb species include *Achlys triphylla*, the species of greatest density and coverage, and many others of distributional groupings 6, 10, and 11, together with some species of groupings 3 in more mesic sites and 12 toward higher elevations. Average composition of these forests is indicated by data for the 1370-1680 m elevation belt in Tables 12-15.

At elevations approaching 1850 m the *A. concolor* forests are usually mixed with *Abies nobilis* Lindl. (*A. procera* Rehd.), sometimes with *Tsuga mertensiana*.

At elevations above 1850 m, subject to differences in exposure and topographic situation, the latter species become the dominants of subalpine forests. At still higher elevations, above about 1920 m, *T. mertensiana*

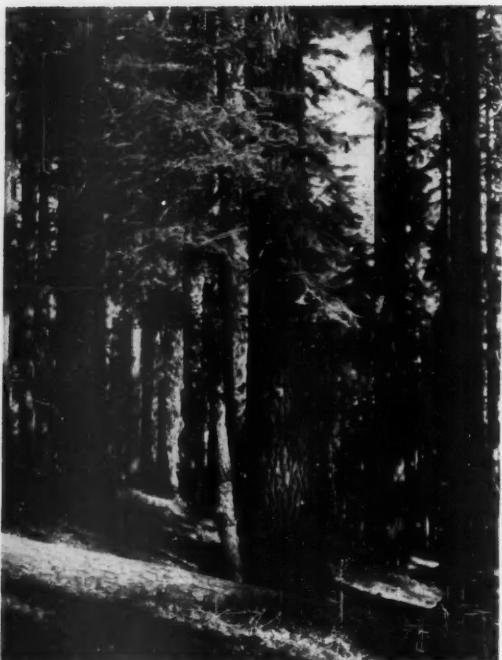


FIG. 13. *Abies nobilis* forest of high elevations in the Siskiyou Mts., Ore. A NE-facing slope on Dutchman Peak, 1920 m, July 14, 1950.

and *A. nobilis* are the only tree species represented in the stands; these are subalpine forests without birches or any other broadleaf associates. Most stands contain both dominants. Proportions of the two are not strongly correlated with elevation or site, suggesting that stand composition is to some extent determined by chance in the newer stands which have developed following fires, or in the primary successions on glacial topography. Within the subalpine forest pattern, however, there is some tendency for *A. nobilis* to predominate toward lower elevations and more xeric sites, *T. mertensiana* toward higher elevations and more mesic sites. Canopy coverages average somewhat less than in the montane forests, and in some stands are below 50%.

Average composition of the subalpine forests is indicated by data for the 1920-2140 and 1680-1920 m elevation belts in Tables 12-15. These forests show a very wide range of herb-stratum coverages—from less than 1% to more than 90%—and great variation in appearance from relatively open stands with lush and floristically rich herb strata to denser stands with almost bare floors of needles and twigs. The former are characterized by a group of herbs—*Arnica latifolia*, the species of highest density and

coverage, *Achlys triphylla*, *Campanula scouleri*, *Are-naria macrophylla*, *Anemone deltoidea*, *Valeriana sitchensis* ssp. *sitchensis*, *Phlox adsurgens*, *Osmorhiza chilensis*, *Hieracium albiflorum*, *Claytonia spathulata*, *Viola glabella*, *Actaea spicata*, *Galium triflorum*, *Trillium ovatum*—with high densities and with constancies of 80-100% in such stands. In stands of low herb coverage some of these, especially *Arnica latifolia*, *Campanula scouleri*, *Hieracium albiflorum*, and *Arenaria macrophylla*, are still present, but represented by few individuals. Along with these, the herb strata include *Chimaphila menziesii*, *Pyrola secunda*, *Pyrola picta*, *Corallorrhiza maculata*, and toward lower elevations, *Chimaphila umbellata* var. *occidentalis*; the evergreen ground heaths are a conspicuous part of the sparse herb strata in such stands but are of low constancy in stands with well-developed herb strata. One may recognize at least three distributional groupings or unions among undergrowth species of these forests (cf. Oosting & Billings 1943), although these groupings intergrade: (1) Species with maximum population levels in stands with rich herb strata, and limited occurrence in stands with poor herb strata and in meadows or other open communities, (2) Species of extensive occurrence in meadows and other open communities, which also occur in stands with rich herb strata (see distributional groupings 11 and 12), and (3) Species which are of greatest importance in stands with poor herb strata. The low coverages of the shrub stratum, in which *Ribes marshallii* is the only important species, are correlated with the herb coverages; in stands with herb coverages over 70%, shrub coverages averaged 5%, in those with herb coverages of 2% or less, 0%. Average undergrowth coverages decrease along the moisture gradient from N- to S-facing slopes and from the 1370-1680 to the 1920-2140 m elevation belt; and at any elevation and exposure are inversely correlated with tree-stratum density.

The general character of the diorite vegetation shown by the mosaic chart is a pattern of mixed evergreen forests at low elevations which is gradually transformed toward higher elevations into montane and subalpine coniferous forest. Apart from the Chamaecyparis-Pseudotsuga stands, the vegetation types form a series of belts or zones toward higher elevations; in life-zone terminology (Hall & Grinnell 1919, Jepson 1923-5, Grinnell 1935, Cooke 1941) the Mixed Evergreen Forest is presumably to be identified with the Upper Austral, the forests of Pseudotsuga and *Abies concolor* with the Transition and those of *A. nobilis* and *T. mertensiana* with the Canadian and Hudsonian zones.

A kind of relative discontinuity, defined by growth-forms and not species distributions, between subalpine forests and those of lower elevations was described by the author for the Great Smoky Mountains (Whittaker 1956). No such relative discontinuity could be detected in the Siskiyou pattern; the Subalpine and Montane Forests are continuous with

one another, and the latter with the Mixed Evergreen Forests. Abrupt forest-edges occur between high-elevation forests and meadows; but within the forests themselves the vegetation on diorite is a single, continuously intergrading pattern from most mesic sites to most xeric, and from lowest elevations to highest. Low-elevation vegetation patterns on serpentine and gabbro are correspondingly continuous; and the more limited samples from higher elevations on serpentine indicate, though they are insufficient to demonstrate, the full continuity of the serpentine pattern.

VEGETATION OF HIGHER ELEVATIONS ON SERPENTINE

The serpentine vegetation, described for elevations of 610-920 m, has much the same character up to elevations of 1100 and 1200 m, and down to elevations of 300 m and less. Toward lowest elevations, however, there is striking expansion of the Jeffrey pine woodlands so that these, rather than the two-phase stands, become the prevailing vegetation type on serpentine slopes of low elevations (Figs. 10, 12).

The *Chamaecyparis*-*P. monticola* stands are more narrowly restricted to ravines than the comparable *Chamaecyparis*-*Pseudotsuga* stands on diorite. Some expansion toward higher elevations occurs, and stands dominated by *Chamaecyparis* with *P. monticola* and *Pseudotsuga* were encountered on slopes and flats up to 1400 m. Such stands had high shrub coverages, 65 and 83% in two samples, with *Quercus chrysolepis* var. *vaccinifolia*, *Lithocarpus densiflora* var. *echinoides*, and *Vaccinium parvifolium* the dominant shrubs, and low herb coverages (1-2%), with various of the species of mesic and submesic stands at lower elevations.

The vegetation types which prevail on intermediate sites and intermediate elevations, and thus have a central position in the Siskiyou serpentine pattern, have been grouped together as the "forest-shrub complex." The diverse stands of this grouping are in general characterized by open canopies of mixed conifers, and well-developed undergrowths in which dominance is shared in varying proportions between evergreen shrubs and grasses or grass-like plants. In stands of higher elevations, 1100-1400 m, *Pseudotsuga* and *P. monticola* are the dominant trees, with *Chamaecyparis* toward more mesic and *P. jeffreyi* toward more xeric sites, *Libocedrus* toward lower and *Abies concolor* toward higher elevations. Undergrowths are of the same general character and composition described for lower elevations, with *Quercus chrysolepis* var. *vaccinifolia* the principal shrub and *Xerophyllum tenax* most conspicuous in the herb stratum. Toward still higher elevations, above about 1400 m, stands of the complex extend upward in subxeric sites between the *A. concolor* forests and pine woodlands. In these stands *Pseudotsuga* and *P. monticola* are dominant, and the two-phase undergrowth is replaced by lower strata of quite different appearance and composition, with *Arctostaphylos*

nevadensis the principal shrub and *Xerophyllum tenax* the principal herb.

At highest elevations, *Pinus monticola* occurs in very open stand above an undergrowth strongly dominated by *Xerophyllum tenax*. Physiognomically such *Xerophyllum*-rich stands have the appearance of pine "steppes." Floristically they are much like the high-elevation Jeffrey pine woodlands to be described, but contain also some species of the *A. concolor* forests. In a stand of the type which was studied, at 2040 m on a west-facing slope of Big Red Mountain, the coverage of *P. monticola* was below 30%, with few stems of *A. concolor* and *P. jeffreyi*. Shrub coverage was 24%, predominantly *Arctostaphylos nevadensis*, but with *Amelanchier gracilis* present; *Xerophyllum* predominated in a floristically rich herb stratum of 57% coverage.

At elevations mostly between 1370 and 1770 m, montane forest stands dominated by *A. concolor* and *Pseudotsuga* with *P. monticola*, *P. jeffreyi*, and *Libocedrus* often present, occur. These are more open stands than the montane forests on diorite, with coverages generally between 40% and 70%. Shrub coverages were rather low and herb coverages high, 13 and 48% in a representative sample, with *Arctostaphylos nevadensis* and *Xerophyllum tenax* the stratal dominants. The latter forms, in many of these stands, an apparently "grassy" undergrowth. Flora of the undergrowth includes both some species characteristic of serpentine and some of those of high-elevation diorite vegetation. At higher elevations closed stands of *Abies nobilis* were encountered in the Observation Peak and Big Red Mountain serpentine areas near Ashland Peak. Physiognomically they differed little from comparable stands on diorite, but many herb species characteristic of high-elevation forests on diorite were not recorded in the stands observed.

Most xeric sites on serpentine are occupied by pine steppes or woodlands at all elevations. Floristic composition of these gradually changes upward from that already described at low elevations to the quite different flora of high-elevation stands. *P. monticola* and *A. concolor* occur in some of the high-elevation Jeffrey pine steppes, and *Libocedrus* is often absent. Shrubs included *Chrysothamnus nauseosus* var. *occidentalis*, *Amelanchier gracilis*, *Ceanothus cuneatus*, *Holodiscus dumosus*, and *Quercus chrysolepis* var. *vaccinifolia*, with coverage below 10%. Grasses were *Melica subulata*, *Sitanion hystrix*, *Festuca ovina*, *Bromus breviaristatus* and *B. carinatus*, and *Trisetum canescens*. *Xerophyllum tenax* was the principal herb species; other herbs shared with the low-elevation serpentine flora included *Cheilanthes siliquosa*, *Monardella odoratissima* var. *glaucia*, *Eriophyllum lanatum* var. *lanceolatum*, *Eriogonum nudum*, *Castilleja miniata*, *Phlox diffusa*, *Achillea lanulosa*, *Phacelia dasypylla* var. *ophitidis*, and *Silene campanulata* var. *orbiculata* Rob. Other species of the high-elevation pine steppes were *Iris chrysophylla*, *Vicia californica*, *Arenaria macrophylla*, *Aster siskiyouensis*,

Pedicularis racemosa, *Anemone quinquefolia*, *Eriogonum aliceae*, *Astragalus whitneyi* Gray, *Orthocarpus copelandii*, *Anemone drummondii*, *Sedum obtusatum* ssp. *boreale* Clausen, *Linum lewisii*, *Pentstemon azureus* ssp. *parvulus* (Gray) Keck, *Eriogonum umbellatum*, *Calochortus elegans* var. *nanus* Wood, *Senecio integerrimus* var. *exaltatus* (Nutt.) Cronq., *Erysimum capitatum*, *Polystichum scopulinum* (Eaton) Maxon, *Aster shastensis* var. *eradiata*, and *Lupinus leucophyllus*.

Sample coverage is inadequate to prepare a mosaic chart for gabbro vegetation. In the low elevations studied, the Chamaecyparis-Pseudotsuga type is more narrowly restricted to ravines than on diorite. Because of the greater openness of the gabbro stands, the sclerophyll-Pseudotsuga is in immediate contact with Chamaecyparis-Pseudotsuga, without an intervening Pseudotsuga-sclerophyll type. The more xeric stands on gabbro, with pines predominant and a quite open sclerophyll stratum, represent a third physiognomic type within the Mixed Evergreen Forests (see Part V).

South of the main study area, in the area of Youngs Peak, Sanger Lake, and Preston Peak, a distinctive high-elevation forest pattern occurs, with varied mixtures of *Picea breweriana*, *Abies concolor* and *A. nobilis*, *P. monticola*, Pseudotsuga, and Libocedrus in rather open stands. In more mesic sites near 1500 m stands of Chamaecyparis with *P. breweriana* and *P. monticola* occur; and in more xeric ones stands of *A. concolor* with Pseudotsuga and Libocedrus. Toward higher elevations true spruce-fir stands occur, dominated by *P. breweriana* and *A. nobilis*, with *P. monticola* also present. Shrub and herb coverages were generally low, with *Vaccinium membranaceum* and *Quercus sadleriana* the principal shrubs, *Achlys triphylla* and *Chimaphila umbellata* var. *occidentalis* the principal herbs. This high-elevation pattern is in some respects intermediate to those of diorite and serpentine. Since observations for middle elevations are lacking, its continuity with the low-elevation pattern described for gabbro cannot be established.

IV. CLIMAX INTERPRETATION

The complex vegetation of the Siskiyous raises several problems of climax interpretation. Those to be discussed are: (1) The role of fire, (2) The question of edaphic climaxes, (3) The basis of comparing climax vegetation for different parent-materials and climates, (4) Gradation of climax vegetation along climatic gradients, and (5) Prevailing or "climatic" climax types for this area.

FIRE EFFECTS AND EDAPHIC CLIMAXES

The forests of the Siskiyous exist in a summer-dry, "Mediterranean" climate. During the dry season the forests are inflammable, and the means of igniting them have not been lacking. Essentially all the low-elevation vegetation described has been burned recently enough for fire-signs to be detected in the form

of charcoal in the soil, bark-burns or burned stumps, or in stand composition; it is believed that no low-elevation stand unaffected by fire was observed. All this vegetation is consequently "disturbed" in this sense; but it does not follow from this that the vegetation is to be interpreted as simply secondary.

Self-maintaining, all-age forest stands show a characteristic J-curve for the relation of numbers of tree stems to diameters of stems. Plotted with numbers of stems on a logarithmic scale, these curves become somewhat convex upward (Whittaker 1956) in the form illustrated in Fig. 14 by no. 8, *Pinus jeffreyi*

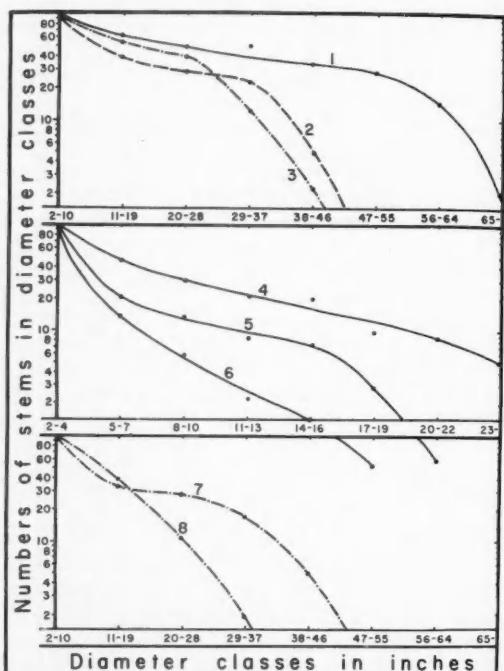


FIG. 14. Stand curves of stem numbers vs. diameters for principal trees at low elevations in the central Siskiyou Mountains, with numbers of stems on a logarithmic scale. Top—*Pseudotsuga menziesii* on quartz diorite (1), olivine gabbro (2), and serpentine (3). Middle—three sclerophylls on diorite, *Arbutus menziesii* (4), *Quercus chrysolepis* (5), and *Lithocarpus densiflora* (6). Bottom—two pines on serpentine, *Pinus lambertiana* (7), and *P. jeffreyi* (8).

on serpentine soils. A wide variety of all-age and presumably climax stands have been found to have curves of this form, though it is by no means the only possible one for climax forests. When stand curves for different species on different soils in the low-elevation Siskiyous are plotted, these curves (with the exception of *P. jeffreyi*) show an interesting and consistent departure from this singly-convex form, as illustrated in Fig. 14.

Increment borings permit some interpretation in relation to tree ages and history of the area. Three

phases of the curves may be recognized in relation to three historic periods: (1) A pre-white period, extending back from somewhat more than a century to several centuries ago, which is reflected in an essentially normal, convex curvature for the largest size-classes in the curves. (2) The historic period of a century or somewhat more, during which the forests were more frequently burned. The resulting reduced reproduction, or heavier mortality among younger trees, is reflected in the flattened intermediate sections of the curves. (3) A more recent period of protection from fire, during which the frequency of fires has been less, and the rate of tree reproduction and survival of younger trees greater, as indicated in the concave, uppermost sections of the curves.

In relation to fire-disturbance and the climax state of these forests, the curves suggest: (1) The older trees are several centuries old; they have survived the more intensive burning by white man and still dominate the upper levels of the tree strata and characterize the vegetation. (2) The general similarity of the curves implies that the different species have been affected in similar ways by increase and decrease of fire frequency. (3) The mixed conifer-sclerophyll dominance of these stands is not a product of more recent, more severe burning; the balance between the two groups in community dominance has been similar, though not necessarily identical, throughout the history represented. (4) The principal effect of less severe fires in this vegetation seems to be not in radical change in community composition, but in reducing the seedling survival, and hence eventually reducing stand density, for both conifers and sclerophylls.

If this vegetation is obviously not, on the one hand, climax vegetation unaffected by fire, neither, on the other hand, is it a vegetation of fire-successions. It may be regarded, rather, as a fire-adapted vegetation of a summer-dry climate, in which fires of varying frequencies and intensities and varying sources—white man, Amerind, and lightning—have for a very long time been part of its environment. If the term “climax” is to be applied in such circumstances, it seems supposititious to apply it to the non-existent vegetation which might develop after centuries of complete fire protection. The climax may better be regarded as that reasonably stable and self-maintaining vegetation which exists in this area, in adaptation to fires and other factors of environment. It may be understood in this case that the climax, or fire-climax, condition embodies a degree of population instability and irregularity resulting from fires affecting different areas in a patch-wise fashion at irregular intervals.

It further appears that vegetation patterns of different parent materials have been similarly affected by fire; no one of them is fire-successional to another. It seems inconceivable that the three vegetation patterns of diorite, gabbro, and serpentine, with their different physiognomies and floras in relation to different nutrient economies, should ever converge

to the same climax even in the absence of fire (Whittaker 1954b). The problem of edaphic climaxes, however, goes beyond the fact that there are three different climax patterns in the same climate. If so marked a difference of climax occurs on these three, and gabbro is intermediate to the other two, it is reasonable to suppose that rocks intermediate to the diorite and gabbro, or gabbro and serpentine observed, would support still different, intermediate vegetation. Granite, the fourth member of the series, is known to support vegetation different from diorite in some areas (Williams 1933). Moreover, the geological diversity of the Siskiyous involves many rock types other than the granite-serpentine series. Close by the diorite area one may observe vegetations of marble, quartzite, slate, and argillite, which differ from the vegetation of diorite and gabbro, especially in more xeric sites. There may be, within the same climate, many climax vegetation patterns differing in different ways and different degrees in response to different parent materials. If one sets aside the vegetation of serpentine as highly anomalous, there still remain the climax patterns, differing in many details, of these other rocks. If one regards these climaxes as part of “the same” climax formation, Mixed Evergreen Forest, one must recognize that they are “the same” in membership in a man-made class of forest communities, but not vegetationally “the same” in plant populations or details of physiognomy. Any statement that one of these vegetations represents the true, climatic climax surely represents an arbitrary choice of what is to be thought a “normal” or “typical” parent material and vegetation pattern.

It was one of the assumptions of the monoclimax theory that the climax, given time for development of a mature soil, should be independent of soil parent material. The diversity of climaxes in the Siskiyous seems to contradict this assumption. The extent to which differences of parent material are reflected in differences of vegetation must be influenced by various factors other than properties of the rocks themselves—climate, physiography, and fire, the general character of the vegetation and soils, floristics and the kinds of plants available to form and dominate communities. Two parent materials may well support different climax vegetations in one set of circumstances, but in another support vegetation which seems not significantly different. But it is suggested that the statement that climax is independent of soil parent material may be replaced by understanding that a significant difference in parent material may usually imply some degree of difference in climax vegetation.

THE COENOCLINE AND CLIMAX COMPARISON

Within each parent material and elevation belt there is conspicuous vegetational gradation from ravines to southwest slopes; the vegetation forms a continuous pattern, or vegetational spectrum, in relation to the topographic moisture gradient. So far as can be determined, in stands not recently and

severely disturbed, vegetation and soil are in the climax condition along the whole of the moisture gradient, at least in the sense that they are in steady-state in relation to the mountain-slope environments in which they exist. "The climax" on a given parent material is consequently not a particular kind of stand, but the whole climax pattern in relation to the moisture gradient (cf. Whittaker 1951, 1956). Considering also elevation and the three soils, climax vegetation in the central Siskiyous may be conceived as a highly diversified, generally continuous, multi-dimensional pattern comprising all the stabilized vegetation described in relation to the moisture, elevation, and diorite-to-serpentine gradients, and other vegetation undescribed.

A principal concern of the present work is with comparison of vegetation patterns of different climates and parent materials. Comparison for different climates, at least, can be based on "climatic climaxes"; but there are limitations to the effectiveness of such comparison, for the community-types to be designated "climatic climax" must be chosen from the vegetational gradient by an ecologist. Much that is significant about vegetational expression of climate may be lost sight of if a single climatic climax type is selected, to the neglect of the rest of the vegetation pattern. Comparison of vegetation from one area to another may be most effective if based, so far as possible, on the whole moisture-gradient patterns for each area.

The expressions community gradient, or pattern, or spectrum, or ecological series have been used in the preceding sections of this work, but a shorter term may be desirable. The term *ecocline* was suggested by Clements (1936), apparently for sequences of climax communities along environmental gradients, but has been little used. The term may be a useful one; and an *ecocline* may be conceived as a gradation in characteristics of ecosystems along an environmental gradient, a gradation which may be underlain or caused by a particular environmental gradient, but is usually expressed in complexly interrelated changes in all aspects of ecosystems. *Ecocline* has been applied also (Huxley 1943) to the genetic gradients or clines within species populations along ecosystemic gradients. For the environmental aspect of the ecosystemic gradient the term *complex-gradient* has been suggested (Whittaker 1954c, 1956), and the term *catena* is in use for the more strictly edaphic aspect (see also terms suggested by Major 1951). For the gradient of natural communities in an ecocline, the term *coenocline* is here proposed; the coenocline and complex-gradient together constitute the ecosystemic gradient or total ecocline.

If the climax on mature, stream-eroded topography is conceived as a "coenocline," then comparison of climaxes for different climates and parent materials may be facilitated by means of further abstraction, to express average or general character of coenoclines. Three approaches to such abstraction

have been suggested by the author (Whittaker 1956). *Average climax composition* is the average composition of climax stands in a given area, or within a given coenocline. *Intermediate climax stands* are intermediate, or median, to the extremes of a coenocline, as determined by the midpoint of a transect, by percentage similarity or coefficient of community comparison with the extremes, or other means. In some cases, as in the kind of topography dealt with here, open east-facing slopes are approximately intermediate to the extremes of the moisture gradient. The *prevailing climax type* is the community-type, whatever the criteria chosen to define it as type, which comprises the majority of the climax stands in a given area or a given coenocline.

These concepts underly the present work in various ways. Vegetation has been sampled, the samples arranged in composite transects, the transects interpreted, and the vegetation itself described, in terms of moisture-gradient coenoclines. Tables 3-11 summarize community composition and the distributions of plant populations in coenoclines in such a way that these may be directly compared from one parent material to another. Tables 12-14 summarize relations of diorite vegetation to elevation in terms of average climax composition, and Tables 3-11 permit a similar summary in relation to the three parent materials at low elevations. The floristic analysis of Part VI is based primarily on species lists for coenoclines, and the comparison of these in terms of life-forms and growth-forms, species-diversities, and areal types. The problem of prevailing climax types for the Siskiyous will be considered in the section which follows.

EAST-WEST GRADATION AND THE PREVAILING CLIMAX TYPE

In order to supplement the work in the central Siskiyous with information on low-elevation climaxes, at least, for other areas of the range, a series of small-scale studies were made from the Coastal Sequoia forests at the western end, to the vegetation of the interior at the eastern end of the Siskiyou Mountains. At each study area six vegetation samples were taken at low elevations, in different topographic positions representing the moisture gradient—ravines, mesic lower slopes, and open NE, E, SE, and S or SSW slopes—along with other notes on the character of moisture-gradient coenoclines. Since each study was a limited transect, this phase of the work was designed as a transect of transects, representing change in low-elevation vegetation patterns along the climatic gradient from the more humid and maritime to the drier and more continental extremities of the Siskiyou Mountains. Some features of the climatic changes along this gradient are indicated in Table 1. The study areas (see Fig. 1), and vegetation patterns, were as follows:

1. Mill Creek State Park, Del Norte County, Calif., in hills or low mountains, about 8 km from the coast,

at elevations of 120-180 m, in coastal Sequoia forest. Stands were strongly dominated by *Sequoia sempervirens* in the upper tree stratum and *Tsuga heterophylla* in the middle tree stratum in all topographic situations. Smaller numbers of *Pseudotsuga menziesii*, *Abies grandis*, and *Chamaecyparis lawsoniana* also occurred, and, in more mesic sites, *Thuja plicata* and *Picea sitchensis*. The lower tree stratum of broad-leaved species included *Lithocarpus densiflora*, *Corylus rostrata* var. *californica*, *Acer circinatum*, and *Umbellularia californica*, but was of very low coverage and density in all sites (averaging only 80 stems/ha). The high shrub stratum, dominated by the arborescent coastal ecotypes of *Vaccinium ovatum* and *V. parvifolium* was, in contrast, highly developed; and in the S-facing stands this stratum formed a dense underbrush, with 3000 and 300 stems/ha respectively for the two species. More important undergrowth plants, besides these, included *Gaultheria shallon*, *Rhododendron californicum*, *Oxalis oregana*, *Polystichum munitum*, *Blechnum spicant* (L.) J. E. Smith, *Viola sempervirens*, *Galium triflorum*, *Trillium ovatum*, *Disporum smithii*, *Whipplea modesta* and, in ravines *Rubus spectabilis*, *Rhododendron occidentale*, and *Adiantum pedatum* var. *aleuticum*. Herb coverage (20-85%) was much higher than in the main Siskiyou study area, shrub coverage was variable from 1-10% in mesic to 70-95% in xeric sites. In stands of mesic flats the shrub cover approached zero and the herb coverage 90% or more, dominated by *Polystichum munitum* and *Oxalis oregana*.

2. In the hills above the Smith River near its junction with the South Fork, at elevations of 180-210 m, about 14 km from the nearest point on the coast, at the inland edge of the Sequoia range, Del Norte County, Calif. Few, widely scattered, large Sequoia occurred in stands strongly dominated in the upper tree stratum by *Pseudotsuga*. The lower tree stratum was dominated by *Lithocarpus* and (in less xeric stands) *Corylus*, averaging around 400 stems/ha each. *Arbutus menziesii*, *Quercus chryssolepis*, and *Cornus nuttallii* also occurred, predominantly in more xeric sites. As in the coast forest, *Vaccinium ovatum* dominated the high shrub stratum, reaching 2500-4000 small stems/ha; *Vaccinium parvifolium* and *Rhamnus purshiana* also occurred, along with numerous stems of *Rhododendron californicum*. Shrub coverages increased from 15-25% to 70-95%, herb coverages decreased from 60-70% to 0-10% along the moisture gradient. In general character this coenocline is one of *Pseudotsuga* forests with limited sclerophyll and heavy evergreen shrub undergrowth, physiognomically very similar to the Sequoia forests of slopes, but with a somewhat greater range of physiognomic and floristic variation along the moisture gradient.

3. Along the Smith River at its junction with the Siskiyou Fork, about 34 km from the coast, Del Norte County, Calif., on lower slopes with elevations between 350 and 450 m on slate soils. Forest stands were dominated by *Pseudotsuga* and, in mesic sites,

Chamaecyparis; of the four coastal conifers only *Tsuga heterophylla* occurred, in small numbers in mesic sites. *Lithocarpus* was the principal small tree, averaging 600 stems/ha; and the other principal small trees of the mixed evergreen forests were present. *Vaccinium ovatum*, *V. parvifolium*, *Rhododendron californicum*, and *Gaultheria shallon* were major shrubs; but the number of *Vaccinium* stems was much lower than in the preceding transects, reaching 250-750 small stems/ha in drier sites. Shrub coverage increased from 25-30% to 50-75%, herb coverage decreased from 30-40% to 0-5% along the moisture gradient. In general character this coenocline is one of mixed evergreen forests, gradating from *Chamaecyparis-Pseudotsuga* stands in ravines to sclerophyll-*Pseudotsuga* stands on xeric slopes, as in the diorite vegetation of the main study area.

4. Low-elevation vegetation already described—that of diorite (and metavolcanic rocks) in the Oregon Caves area, Josephine County, Ore., at 460-760 m, about 75 km from the coast—may serve as the fourth transect of the series. Sclerophyll density was still higher than in the Siskiyou Fork transect—averaging 800 stems/ha for *Lithocarpus* and 600 stems/ha for other species. Deciduous small trees averaged about as dense (250 stems/ha) as at Siskiyou Fork. *Vaccinium ovatum*, *V. parvifolium*, and *Rhododendron californicum*, on the other hand, were infrequent. Herb coverage decreased from 8-20% to 0-8% along the moisture gradient, and shrub coverage was between 10 and 40% in most stands.

5. Above Sturgis Creek, near Steve Peak, Josephine County, Ore., 15 km east from the Oregon Caves area, on metavolcanic rocks at elevations of 850-980 m. The vegetation was also mixed evergreen forest in predominant character, but showed effects of somewhat drier and more continental climate in a number of features. Three dominant species of the preceding vegetation patterns—*Chamaecyparis lawsoniana*, *Lithocarpus densiflora*, and *Gaultheria shallon*—were absent. Sclerophyll density, which had risen in the preceding series of transects, fell to an average of 500 stems/ha (from about 700 at comparable elevations in the Oregon Caves area), predominantly *Quercus chryssolepis* with smaller numbers of *Arbutus menziesii* and *Castanopsis chrysophylla*. Numbers of deciduous tree stems were higher—250 stems/ha in contrast to about 120 at comparable elevations in the Oregon Caves area—and included more numerous stems of *Quercus kelloggii* Newb. in more xeric stands. Important shrubs included *Berberis nervosa*, *Rhus diversiloba*, *Rubus vitifolius*, and *Rosa gymnocarpa*; they included also species rare in or absent from the Oregon Caves diorite transect—*Rubus leucodermis* and *R. parviflorus*, *Rosa spaldingii*, *Berberis piperiana*, and in xeric sites *Ceanothus integrifolius* and *Arctostaphylos viscosissimum* Peck. The herb stratum included most of the species familiar in the Oregon Caves area and some additional ones. Herb coverages decreased from 7-18% in more mesic to 0-5% in more xeric sites; shrub coverage was gen-

erally between 10 and 40%. Difference from the Oregon Caves diorite vegetation was most conspicuous in the south-facing slopes, where *Pseudotsuga* shared dominance with *Pinus ponderosa* and *P. lambertiana* in open stands with well developed shrub strata. Pine dominance appeared to be at least partly a consequence of fire; but such stands are not encountered even as a consequence of burning in the Oregon Caves area on metavolcanic rock or diorite.

6. Near Beaver Creek, 105 km from the coast, on granite at elevations between 640 and 850 m, Jackson County, Oregon. More mesic stands were dominated by *Pseudotsuga* with a poorly developed sclerophyll layer; the (fire-affected) stands of south-facing slopes were dominated by *Pinus ponderosa* and *Pseudotsuga* in open growth. Representation of sclerophyll species (*Q. chrysolepis* and *Arbutus*) was still lower—200 stems/ha; representation of deciduous trees other than oaks only 170 stems/ha. *Quercus kelloggii* and *Q. garryana*, however, were in this area major small-tree species, contributing about 220 stems/ha on the average, with populations of 270 and 550, 150 and 390 stems/ha in the south-slope samples. Important shrubs included *Berberis nervosa* and *B. piperiana*, *Rubus vitifolius* and *R. leucodermis*, *Rhus diversiloba*, *Rosa gymnocarpa* and, in xeric sites, *Ceanothus integerrimus*, *Arctostaphylos viscissimum* and *A. viscida*. Herb stratum coverages decreased from 12-25% to 5-12%, shrub coverages increased from 7-25% to 20-50% along the moisture gradient. In general character the ecocline is one of *Pseudotsuga* forests with sclerophylls gradating into *Pinus*-*Pseudotsuga*-deciduous oak forests in xeric sites. The transition from mixed evergreen forest to oak woodland is represented in approximate equality of sclerophylls and deciduous oaks in the pattern as a whole, and predominance of the oaks over sclerophylls in more xeric sites.

7. The final transect of the series was near Emigrant Creek, near Steinman in Jackson County, Oregon, at elevations between 820 and 1070 m, on andesite, 140 km from the Pacific Coast. Stands of ravines and mesic lower slopes were dominated by *Pseudotsuga* with *P. ponderosa* and *Libocedrus* present. Deciduous species in these coniferous forests included *Acer macrophyllum*, *Alnus rhombifolia*, and *Fraxinus oregana*. On the open NE slope *Pseudotsuga* shared dominance with *P. ponderosa* and *Libocedrus* in open stand, with a well-developed lower tree stratum (50% coverage) dominated by *Quercus garryana*. The conifers were absent from less mesic stands (open E and SE slopes), except for scattered *P. ponderosa*; these stands were oak woodlands of *Q. garryana* and *Q. kelloggii* with moderate tree (65 and 45%) and grass (20 and 60%) coverage. Sclerophylls were unimportant in either coniferous forest or oak woodland; only a few stems of *Arbutus* were recorded in the former. *Ceanothus integerrimus*, *Arctostaphylos viscida*, and *Cercocarpus betuloides* were important high shrubs. Oak coverage decreased while grass coverage increased toward most xeric sites,

and open S and SW slopes supported grassland without or with widely scattered oaks. The grassland, severely disturbed, was dominated by *Elymus caput-medusae* where analyzed. This final vegetation pattern represents shrinkage of conifer forest into mesic sites, reduction of the sclerophyll element to insignificance, and appearance of the oak woodland and valley grassland communities of the Interior as part of the ecocline, at the eastern end of the Siskiyous. The transitions from the Siskiyous vegetation to that of the Cascades and Interior are more complex than this single transect indicates; but the pattern described is that characteristic of low elevations in the interior valleys of the Rogue and Umpqua Rivers (Peck 1941).

Of the conclusions from this climatic transect, a series of trends may first be observed:

a) Stature and coverage of the coniferous high-tree stratum decreases progressively from the great *Sequoia* forests eastward. In inverse relation to this, the density of deciduous broadleaf trees increases toward the east. Maximum densities of sclerophylls (and of all broadleaf trees taken together) were in the Oregon Caves area near the middle of the transect, and the sclerophylls decrease toward both ends of the transect.

b) Both shrub and herb coverages decrease from the *Sequoia* forests to the middle of the transect, then increase again to the eastern end of the transect (though these trends are complicated by variations with site in a given area). Undergrowth coverages thus show some inverse correlation with development of the sclerophyll stratum.

c) Floristic trends in representation of life-forms, growth-forms, and areal types will be discussed in Part VI.

d) Distributions of species change in relation to the topographic gradient. (1) There is a general narrowing of species amplitudes toward the east. Many species occupy the whole of the topographic moisture gradient at Mill Creek, apparently none more than part of the gradient at Emigrant Creek. (2) Distributions of species (and community-types) shift along the moisture gradient in such a manner as to compensate for more or less humid climates. Species of wide amplitudes near the coast are increasingly restricted to the mesic end of the gradient toward the interior; species occurring in the interior transects are increasingly displaced toward the xeric end of transects nearer the coast. (3) Ecotypic populations show complex relations to parent materials and the climatic gradient. Many species largely restricted to "special" parent materials (serpentine, gabbro, quartzite, slate, argillite, marble), generally with more open or xeromorphic vegetation in one area, occur in the vegetation of "normal" parent materials (granite, diorite, andesite, metavolcanic rocks) in a drier and more continental climate toward the east. In contrast to this, several species (*Vaccinium parvifolium*, *V. ovatum*, *Vancouveria chry-*

santhia, *Galium ambiguum*, *Polygala californica*) had ecotypic populations widely distributed in the humid coastal forests, and other populations largely restricted to serpentine and gabbro in the drier climate of the main study area.

Second, the results indicate that the prevailing climaxses of the Siskiyous at low elevations are: (1) Sequoia forest near the Coast, (2) a belt of coastal Pseudotsuga forest within this, (3) Mixed Evergreen Forests over the greatest part of the range between these coastal Forests and the interior valleys, (4) Oak Woodlands in these valleys at the eastern end of the range. The Oregon Caves study area on diorite, within the area of maximum development of the sclerophylls, is thought as "representative" of the mixed evergreen forests at their best development in the Siskiyous as any area known to the author. In relation to the Mixed Evergreen Forest region as a whole, however, it represents not average or median conditions, but those of maximum stand density toward the northern and mesophytic limits of these forests.

A final result of significance is the continuity of vegetational change along the climatic gradient studied (cf. Whittaker 1956). This continuity can scarcely be perfect, considering the irregular topography and effects of parent materials. But with allowance for these, the climatic gradient was expressed in gradual transformation of communities in both physiognomy and floristic composition, in shifts of position along the moisture gradient for both species populations and community-types, and not in abrupt transition. This continuity is the more impressive in that four formations—the Coast Forest, Mixed Evergreen Forest, Oak Woodland, and Valley Grassland—are involved. One can divide the continuity by prevailing climaxes and major community-types, but these approaches do not clarify the underlying quantitative relations. The approach through comparison of moisture-gradient patterns makes possible some quantitative analysis of the gradual transformation of community-types and vegetation patterns along a climatic gradient.

V. PROBLEMS OF CLASSIFICATION

There are many ways of classifying vegetation; and most studies are influenced not merely in form of presentation, but in the way vegetation is observed and sampled, by the author's particular approach to classification. One object of the present study was to take samples which could be used to compare different approaches to classification. The preceding description embodies the author's own approach through physiognomy and dominance. The same material may be considered, however, in relation to several major vegetation units—the formation, dominance-type, sociation, association, and union.

FORMATIONS

A formation is a grouping of communities which are similar in physiognomy and in broader environmental relations (cf. Beadle & Costin 1952, Whittaker

1957). Four formations—Coast Forest, Mixed Evergreen Forest, Oak Woodland, and Valley Grassland—appear in the climatic transect; three other forest formations—Montane Forest, Subalpine Forest, and Pine Woodland—occur in other environments. The Montane Forests and Subalpine Forests are in these mountains physiognomically continuous with one another. If they are to be separated as formations, as is customary, it must be on the basis of environmental relations, primarily elevation, and broad floristic and geographic relations, to the western Montane Forests and circumboreal taiga, not physiognomy. The yellow pine woodlands or pine steppes of the western states are often treated as part of the Montane Forest Formation. Their physiognomy is fundamentally different, however; and they may well, even though they intergrade with the closed Montane Forests, be regarded as a separate formation. Pine woodlands appear both on serpentine in the central Siskiyous (dominated by *P. jeffreyi*) and in drier situations of middle and higher elevations in the eastern part of the range (dominated by *P. ponderosa*).

The Mixed Evergreen Forests have affinities with the sclerophyll vegetation complex of California. Two major community-types have been recognized in this complex—the chaparral of shrubs and the broad sclerophyll forest dominated by trees (Cooper 1922, Oosting 1956). Among the associations of the broad-sclerophyll forest formation Cooper (1922) recognized one, the *Lithocarpus densiflora*-*Quercus chryssolepis*-*Arbutus menziesii* association, as characteristic of lower altitudes of the north Coast Ranges of California. He further observed that this association is itself somewhat a transition between broad-sclerophyll and coniferous types; for it rarely occurs without a sprinkling of conifers, especially Pseudotsuga, and its principal species occur commonly as an understory in the Pseudotsuga and Sequoia forests. Cooper's *Lithocarpus*-*Quercus*-*Arbutus* association is part of the Mixed Evergreen Forest, as designated by Munz & Keck (1949, 1950, 1959) and understood in this paper. The sharing of dominance between evergreen needle-leaved and sclerophyllous trees, and the transitional relation to the sclerophyll vegetation on the one hand, the Coastal and Montane Forests on the other, are essential features of this community-type.

The Mixed Evergreen Forest is unrecognized as a major community-type in its own right in many accounts (Weaver & Clements 1938, Oosting 1956). It is evidently transitional between sclerophyll and conifer forests, but only in the sense that many major community-types are transitional between other community-types. More critical than its transitional relation in evaluating the Mixed Evergreen Forest are the facts that: (1) It is itself a grouping of a number of dominance-types or associations. (2) It is the regional climax of an extensive area of the Klamath Region and north California Coast Ranges. (3) It possesses, especially on some parent materials,

a wealth of character-species largely or wholly restricted to it. The author advocates recognition of the Mixed Evergreen Forest as one of the major community-types of western North America and, because its definition is physiognomic, prefers to regard it as a formation. The characterization suggested for it is: mixed forest with an upper tree stratum of needle-leaved evergreen or coniferous and a lower tree stratum of broad-leaved evergreen or sclerophyllous species, but with these varying widely in coverage and density in different stands. Either one or both of these strata may be either relatively dense or quite open, but as both become open the formation gradates into pine-oak woodland.

A much more complex pattern of physiognomic types of vegetation exists in the western states than in the eastern, and in many cases the formations seem to intergrade as parts of longer physiognomic continua. These circumstances suggest that the approach developed by Beard (1944, 1955) in the tropics may be appropriate to western vegetation. The approach permits the conception of physiognomic relations of vegetation through larger numbers of more narrowly defined formations, arranged in formation-series complexly intersecting one another in relation to major gradients of environment. The author is not prepared to erect a system of formations and formation-series for the whole of the Klamath Region. The material discussed suggests, however, these major relations on more typical soils: (1) At low elevations, from the Coast inland, with decreasing precipitation and increasing continentality—Coast Forest, Mixed Evergreen Forest, Oak Woodland, and Valley Grassland. (2) At low elevations, in maritime environments near the Coast, with increasingly humid climates—Chaparral, Broad-Sclerophyll Forest, Mixed Evergreen Forest, and Coast Forest. (3) In the central Siskiyou Mountains, from low elevations to high—Mixed Evergreen Forest, Montane Forest (and ponderosa pine woodland in some drier sites), Subalpine Forest.

DOMINANCE-TYPES AND SOCIATIONS

Within the formations accepted by the author for the Siskiyou Mountains, various dominance-types defined by species dominance may be recognized. Within the Subalpine Forests *Abies nobilis* and *Tsuga mertensiana* dominance-types, within the Montane Forests *Abies concolor* and *Pseudotsuga menziesii*, dominance-types, within the Coast Forests *Sequoia sempervirens* and *Pseudotsuga menziesii* dominance-types may be distinguished. Such types defined by a single dominant species are "consociations" in Clementsian terminology (Clements 1928, 1936, Weaver & Clements 1938).

The author attempted to classify samples from mixed evergreen forests by combinations of dominant species, to see whether the stands would fall naturally into groups representing well-defined dominance-types. They did not, and a large number of types intergrading with one another resulted. These may

be grouped into three more broadly defined dominance-types: *Chamaecyparis-Pseudotsuga* forests of mesic sites, with deciduous and sclerophyll lower-tree strata, forming closed stands on diorite and more open ones with *Libocedrus* and *P. lambertiana* on gabbro. (2) *Pseudotsuga-Lithocarpus-Arbutus* forests, with other sclerophylls present and in some circumstances dominant and with wide variation in coverage of the tree strata, occurring along most of the moisture gradient on diorite and in less xeric sites on gabbro. *Pseudotsuga-sclerophyll* and *sclerophyll-Pseudotsuga* physiognomic subtypes are distinguished within this dominance-type (Part III). (3) Open *Pinus-Pseudotsuga-Q. chrysolepis-Arctostaphylos* forests of more xeric sites on gabbro and eastward from the main study areas.

Vegetation types defined by dominant species of the various strata, or by combinations of stratal unions, are properly termed *sociations* (Du Rietz 1930, 1936, Nordhagen 1937, 1943, Braun-Blanquet 1951, Hanson 1953, Böcher 1954); such units permit a finer division of the vegetation into more numerous types than dominance-types based on the uppermost stratum alone. An effort was also made to classify the Siskiyou samples by stratal dominants, with results similar to those on dominance-types: a very large number of sociations, intergrading with one another through various combinations of dominance in the different strata, differing widely in extensiveness or importance, many of them of no observable significance in relation to environmental difference, resulted. Much of the Siskiyou vegetation is relatively rich in species and shows no well-defined dominance in the lower strata. Certain community-types with well-marked stratal dominance (e.g. *Abies concolor-Arctostaphylos nevadensis-Xerophyllum tenax* forest and *Pinus jeffreyi-Arctostaphylos viscida-Stipa lemmoni* woodland on serpentine, *Sequoia sempervirens-Tsuga heterophylla-Vaccinium ovatum-Polygalis munitum* Coast Forest) are conveniently defined in the manner of sociations. But the experiments with classification of Siskiyou vegetation support the European experience, that the *sociation* is a unit best suited to communities with marked stratal dominance such as occur, for the most part, in floristically poor vegetation.

ASSOCIATIONS

The principal vegetation unit of phytosociology is the *association*, defined primarily by character-species—species of narrower ecological amplitudes which are largely or wholly restricted to or, at least, centered in, stands of a given community-type (Braun-Blanquet 1932, 1951). The samples taken from the Siskiyou vegetation were intended to be relatively complete floristically and suitable for classification into associations, although they include no data on bryophytes and lichens. The transects provide an effective picture of the distributional relations which underlie problems of floristic classification.

The transects show that population centers or distributional modes, and also the limits of distributions, are scattered along the various gradients studied. Species populations do not form well-defined groups of character-species with similar or congruent distributions. Character-species groupings must be created by the phytosociologist, and there are a number of ways in which the species of a given vegetation pattern may be grouped without violating their distributional relations (cf. Whittaker 1956). It is consequently often possible to choose character-species groupings which fit into community-types recognized initially by physiognomy, dominance, and environmental relations. It cannot be assumed that these units, secondarily defined by floristic composition, will be the same as the units which would be recognized by a phytosociologist who sought to base his work primarily on floristic composition. It is at least possible, however, to bring these two major approaches to vegetation classification into some accommodation to each other. Full discussion of the floristic approach to classification of this vegetation is outside the scope of the present monograph; but

character-species groupings by which the author's community-types may be defined as associations (or, more probably, higher units of this system) are indicated in the following section on distributional groupings.

QUANTITATIVE APPROACHES TO CONTINUITY AND SPECIES GROUPING

The work on classification included also experiments on quantitative methods by which relative discontinuities and natural clusters of species might be objectively revealed from the transect tables. The first of these methods is designed as an aid to the recognition of different rates of change between community-types. Percentage similarities (see Part VI) were computed between successive steps of the transect tables, for each of the three strata on each of the three parent materials. The resulting values are plotted in line graphs (upper halves of Figs. 15-17). Most of the graphs are of the form to be expected in continuously gradating vegetation—points generally at the same level, but with some zig-zag up and down due to chance variations in stand composition. Low points appear between the first and second steps on gabbro and serpentine. The change indicated is that from riparian communities of wet

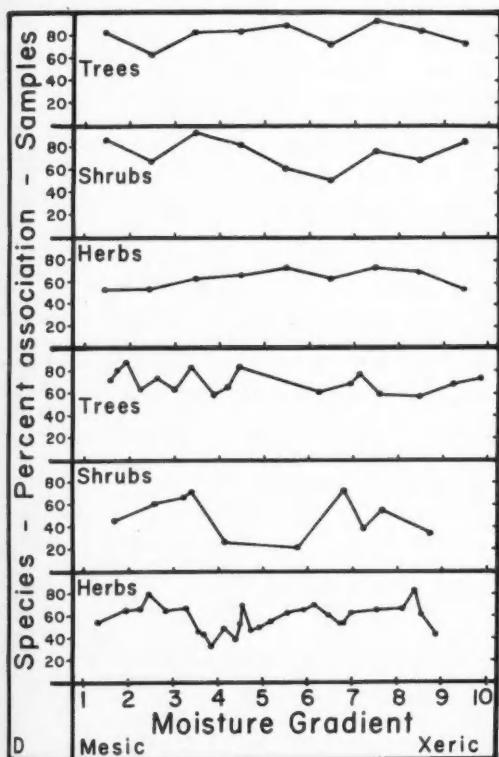


FIG. 15. Sample and species associations in a transect of the moisture gradient at low elevations on diorite. Above—percentage similarities of successive steps of the transect, for the tree, shrub, and herb strata. Below—percentage similarities of distributions of pairs of species, for the three strata.

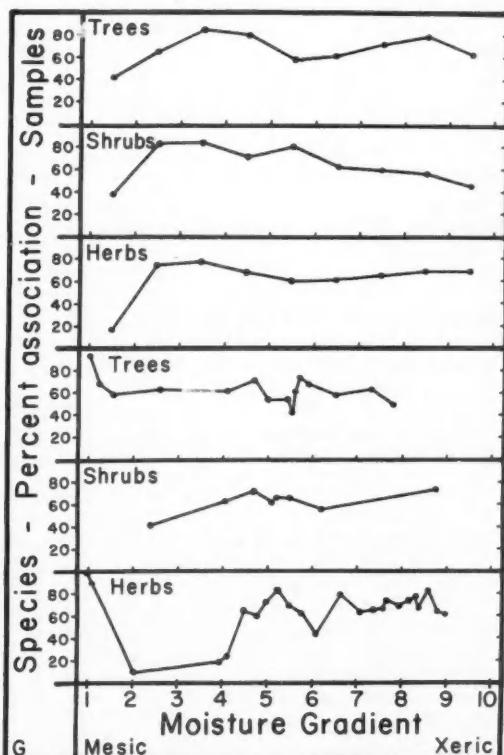


FIG. 16. Sample and species associations in a transect of the moisture gradient at low elevations on gabbro.

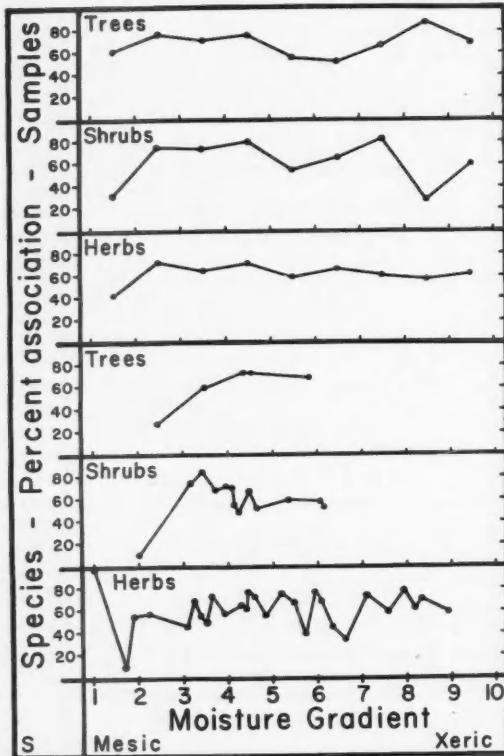


FIG. 17. Sample and species associations in a transect of the moisture gradient at low elevations on serpentine.

soils along stream-sides to the communities of mesic slopes above the ravines. It may be interpreted as a steeper gradient of community composition in response to a steeper environmental gradient, rather than as a vegetational discontinuity occurring along a uniform gradient. Two other low points—in the shrub strata between steps 8 and 9 of the serpentine transect, 6 and 7 of the diorite transect—appear to result from sample irregularity without vegetational discontinuity, and suggest caution in the interpretation of such data.

The other technique is designed to reveal natural clusters of species populations in the transects. For each species represented by significant numbers of individuals, two values were computed: (1) The mean position of the population in relation to the transect

gradient, computed from $\frac{\sum nx}{\sum x}$, in which x is the num-

ber of individuals of the species in a given step of the transect, n the number of the step in the transect. These values may bear little relation to population centers or modes, but provide an indication of relative positions along the gradient. (2) The percentage similarity of species distributions for all pairs

of species, by the formula $PS_d = \sum \min(a, b)$, in which a is the per cent of the total population of species A in the transect table which occurs in a given step of the table, and b the same for species B (Whittaker & Fairbanks 1958). Percentage similarities of distribution were computed for all possible pairs of species in a given stratum for a given transect table, and the resulting values were arranged in matrices or Kulczyński triangles. Species were then arranged in sequence on the basis of their "mean positions"; and for each pair of species contiguous in the sequence, a point was entered in the species-association diagrams indicating the distributional association value from the matrix on the ordinate, the mid-point between the mean positions of the two species on the abscissa.

Natural clusters of species should appear as clusters of points in the diagram which are both of high values for distributional similarity, and close together in mean position along the abscissa. Individualistic scattering of species distributions should be reflected in points which are neither very high nor very low but moderate and variable, forming an irregular, zig-zag line. It is the latter pattern which appears in the results, in the lower halves of Figs. 15-17. The species of the most distinctive union of the vegetation described, the shrubs of the two-phase serpentine vegetation, do not show very strong distributional association with one another, or generally higher association with one another than with other shrubs with distributions overlapping theirs. The graphs do indicate distinct clusters of undergrowth species in ravines (points 1 on the transects); these clusters again represent the distinctive stream-side communities. The species which these clusters comprise are easily shown to be individualistic in their distributional relations to elevation, the three soil parent materials, and geography; they are clustered in relation to the range of environments represented by a given transect, but not in their over-all distributions. Results thus support conclusions suggested in a previous study (Whittaker 1956:22). Natural clusters are weakly developed in, or absent from, most of the vegetation studied, but may be present in some circumstances. Where they occur, as in the stream-side communities, they are not exceptions to the principle of species individuality; and their recognition is dependent on the range of conditions over which distributional relations of species are observed. What is a natural cluster in relation to one transect or one local vegetation pattern may not be a natural cluster in a broader range of vegetational observation.

DISTRIBUTIONAL GROUPINGS

Species occurring in significant numbers in the principal study area, at low elevations on serpentine or gabbro or at any elevation in forests on diorite, have been classified into distributional groupings. Despite the arbitrariness of such groupings, they may have real usefulness; they are used here to summarize

distributional relations of the Siskiyou species dealt with, to avoid repetitious listing of species in the vegetation descriptions, and to provide some definition of major community-types by character-species groupings. A distributional grouping, within a given stratum or life-form, is regarded as a *union* (Lippmaa 1935, 1939, Du Rietz 1936, Oosting & Billings 1943, Billings 1945, Braun-Blanquet 1951:47-49, Daubenmire 1952, Whittaker 1956). The groupings given here are based on broad relations to topographic moisture gradients, elevation, and parent material as represented in the transects; they are not intended to reflect any distributional relation outside the range of environments covered by these transects. Most species can be found outside the indicated distribution patterns, which are intended to represent more frequent occurrence in communities, and to exclude very scattered occurrence at transect constancies of less than 6 or 8%. Certain species with complex distributional relations, or morphologically distinct populations in different habitats, are listed more than once.

1. Riparian species, occurring predominantly on or near stream-banks in ravines at lower (and middle) elevations, in forests in which *Chamaecyparis lawsoniana* occurs as a dominant.

On diorite (character-species of Chamaecyparis-Pseudotsuga forests) at lower, or at middle (*) elevations: Herbs—*Aralia californica*, *Athyrium felix-femina*^o, *Carex laeviculmis*^o, *C. mertensii*^o, *Claytonia spathulata*, *Listera cordata*, *Luzula parviflora*^o, *Pleurozopogon refractus*^o, *Satureja douglasii*, *Tolmiea menziesii*^o.

On diorite and gabbro (character-species of Chamaecyparis-Pseudotsuga forests): Trees—*Alnus rhombifolia*, *A. rubra*. Herbs—*Boyninia elata*, *B. major*.

On gabbro (character-species of Chamaecyparis-Pseudotsuga forests): Herbs—*Epipactis gigantea*, *Erigeron cervinus*, *Juncus ensifolius*, *Peltiphyllum peltatum*, *Woodwardia fimbriata*.

On gabbro and serpentine (occurring in Chamaecyparis-Pseudotsuga and Chamaecyparis-*P. monticola*-Pseudotsuga ravine forests of these two parent materials): Shrub—*Rhododendron occidentale*. Herbs—*Carex debiliformis*, *Cypripedium californicum*, *Darlingtonia californica*, *Eriophorum crinigerum* (Gray) Beetle, *Habenaria sparsiflora*, *Rudbeckia californica*, *Tofieldia glutinosa* ssp. *occidentalis* (Wats.) C. L. Hitchc.

On serpentine (character-species of Chamaecyparis-*P. monticola*-Pseudotsuga forests): Shrubs—*Physocarpus capitatus*, *Rosa californica*. Herbs—*Carex angustior*, *Castilleja miniata*, *Galium multiflorum*, *Helenium bigelovii*, *Lilium occidentale*, *Trillium rivale*.

2. Lower-elevation mesic species of diorite, or diorite and gabbro (*), centered in Chamaecyparis-Pseudotsuga forests but occurring also in more mesic Pseudotsuga-sclerophyll forests: Trees—*Acer circinatum*, *Amelanchier florida*^o, *Salix* sp., *Taxus brevifolia*. Shrubs—*Gaultheria shallon*^o, *Philadelphus lewisii*, *Vaccinium parvifolium*. Herb—*Polystichum munitum*.

3. Mesic forest species of lower and middle elevations on diorite, or diorite and gabbro (*), centered in and character-species for Chamaecyparis-Pseudotsuga forests, but occurring also in more mesic Pseudotsuga-sclerophyll forests at lower, and montane forests at middle, elevations, and in many cases in lower subalpine forests: Trees—*Acer macrophyllum*^o, *Corylus rostrata* var. *californica*. Shrubs—*Holodiscus discolor*^o, *Pachystima myrsinites*, *Rhododendron californicum*. Herbs—*Cephalanthera austinae*, *Coptis laciniata*, *Heuchera micrantha*, *Linnaea borealis*, *Listera caerulea*, *Mitella ovalis*, *Pyrola bracteata*, *Senecio bolanderi*, *Viola sempervirens*.

4. Mesic species of low elevations on serpentine (character-species of the forest-shrub complex) or on serpentine and gabbro (*): Tree—*Pinus monticola*. Shrubs—*Amelanchier gracilis*^o, *Berberis pumila*, *Garrya buxifolia*, *Juniperus sibirica*, *Lithocarpus densiflora* var. *echinoides*, *Quercus chryssolepis* var. *vaccinifolia*, *Rosa gymnocarpa*, *Umbellularia californica* (shrubby population), *Vaccinium parvifolium*. Herbs—*Angelica arguta*, *Antennaria suffruticosa*, *Arnica spathulata* var. *eastwoodiae*^o (Rydb.) Mag., *A. parviflora* ssp. *parviflora*^o, *Aster brickelloides* Greene, *Epilobium rigidum*, *Haplopappus ramosus* ssp. *congestus* (Greene) Hall, *Ligusticum apium*, *Lilium howellii*, *Lomatium howellii*^o, *Lotus oblongifolius*^o, *Lupinus latifolius* var. *columbianus*, *Sancicula peckiana*, *Tauschia glauca*, *Vancouveria chrysanthia*.

5. Species with broad moisture-gradient distributions at lower elevations on diorite, or diorite and gabbro (*), character-species of Mixed Evergreen Forests in a broad sense, occurring also in Chamaecyparis-Pseudotsuga forests: Trees—*Arbutus menziesii*^o, *Castanopsis chrysophylla*, *Cornus nuttallii*^o, *Lithocarpus densiflora*^o, *Quercus chryssolepis*^o. Shrubs—*Berberis pumila*, *Rhus diversiloba*^o, *Symporicarpus hesperius* G. N. Jones, Herbs—*Allotropa virgata*^o, *Lathyrus pauciflorus*, *Lonicera hispida*^o.

6. Species with broad moisture-gradient distributions at lower and middle elevations on diorite, or on diorite and gabbro (*), occurring in mixed evergreen and Chamaecyparis-Pseudotsuga forests of lower elevations and montane forests of middle elevations, and in many cases extending into lower subalpine forests: Shrubs—*Berberis nervosa*, *Rosa gymnocarpa*, *Rubus parviflorus*^o, *R. vitifolius*. Herbs—*Achlys triphylla*, *Adenocaulon bicolor*, *Apocynum pumilum*, *Bromus suksdorffii*, *Galium triflorum*, *Festuca occidentalis*^o, *Goodyeara decipiens*, *Iris chrysophylla*^o, *Melica harfordii*.

7. Species with broad moisture-gradient distributions at low elevations on gabbro and serpentine:

On gabbro: Trees—*Pinus ponderosa*, *Umbellularia californica*. Shrubs—*Garrya fremontii*, *Vaccinium ovatum*. Herbs—*Carex multicaulis*, *Festuca californica*, *Galium bolanderi*.

On gabbro and serpentine: Tree—*Libocedrus decurrens*. Shrubs—*Convolvulus polymorphus*, *Holodiscus dumosus*, *Rhamnus californica* var. *occidentalis*. Herbs—*Galium ambiguum*, *Polygala californica*, *Polygonatum munatum* var. *imbricans*, *Pyrola dentata*, *Schoenolirion album*, *Viola lobata*, *Xerophyllum tenax*.

On serpentine: Tree—*Pinus attenuata*. Shrub—*Arctostaphylos nevadensis*. Herbs—*Balsamorhiza deltoidea*, *B. platylepis*, *Calamagrostis koeleroides*, *Cordylanthus viscidus*, *Hieracium cynoglossoides* var. *nudicaule* Gray, *Iris bracteata*, *Lotus crassifolius*, *Phlox speciosa*, *Sedum laxum*.

8. Species of lower elevations in more xeric sites on diorite and gabbro, character-species of sclerophyll-Pseudotsuga forests (including *Pinus*-Pseudotsuga-*Quercus*-*Arctostaphylos* forests on gabbro):

On diorite: Herbs—*Collomia heterophylla*, *Cypripedium fasciculatum*, *Festuca rubra*, *Madia madioides*, *Psoralea physodes*, *Tauschia kelloggii*.

On diorite and gabbro: Tree—*Quercus kelloggii*. Herbs—*Boschniakia hookeri*, *Campanula prenanthoides*, *Pteridium aquilinum* var. *pubescens*.

On gabbro: Tree—*Arctostaphylos cinerea*. Shrub—*Ceanothus integerrimus*. Herb—*Hieracium bolanderi*.

9. Species of more xeric sites at lower elevations on serpentine, or on serpentine and gabbro (*). The former are character-species for the *Pinus jeffreyi* woodlands on serpentine; the latter occur also in *Pinus*-Pseudotsuga-*Quercus*-*Arctostaphylos* forests on gabbro: Tree—*Pinus jeffreyi*. Shrubs—*Arctostaphylos viscida*, *Quercus garryana* var. *breweri*. Herbs—*Achillea lanulosa*, *Agrostis hallii**, *Bromus brevioristatus*, *Calochortus howellii*, *C. tolmiei*, *Ceanothus pumilus**, *Cheilanthes siliquosa*, *Dianthonia californica*, *Elymus glaucus*, *Epilobium paniculatum* var. *hammondi*, *Erigeron foliosus* var. *confusus**, *Eriogonum nudum**, *E. ternatum* Howell, *Eriophyllum lanatum* var. *achilleoides**, *Horkelia sericata*, *Koeberlinia cristata*, *Lomatium macrocarpum*, *L. triternatum*, *Melica geyeri*, *Monardella odoratissima* var. *glaucia**, *M. villosa* var. *subserata**, *Pentstemon laetus* ssp. *roezlii* (Regel) Keck, *Perideridia oregana*, *Phacelia dasypylla* var. *ophitidis*, *Senecio fastigiatus**, *Sidalcea malvaeflora* ssp. *elegans** (Greene) C. L. Hitch., *Sitanion jubatum*, *Stipa lemmonii**, *Zygadenus micanthus*.

10. Species occurring at or centered in middle elevations, 1200-1800 m, on diorite, character-species for the montane forests dominated by *Pseudotsuga menziesii* and *Abies concolor*. Many of these species extend into low elevations in Chamaecyparis-Pseudotsuga forests, and some (*) were recorded frequently from open situations as well as forests: Trees—*Abies concolor*, *Acer glabrum* var. *douglasii*. Shrub—*Rubus niveus*. Herbs—*Actaea spicata* L., *Anemone deltoidea*, *Asarum caudatum*, *A. hartwegii*, *Circaeal alpina* var. *pacifica* (Asch. & Mag.) M. E. Jones, *Clintonia uniflora*, *Corallorrhiza striata*, *Festuca subulata*,

liflora, *Habenaria sparsiflora*, *Hackelia jessicae**, *Lathyrus polyphyllus*, *Nemophila parviflora*, *Osmorhiza occidentalis**, *Tiarella unifoliata*, *Vancouveria hexandra*, *Viola glabella**, *Vicia californica*.

11. Species of middle- and higher-elevation forests, occurring in both montane and subalpine forests, or both these forests and more open situations (*): Shrubs—*Quercus sadleriana*, *Ribes marshallii*, *R. viscosissimum*, *Symporicarpos rivularis*, *Vaccinium membranaceum*. Herbs—*Agastache urticifolia**, *Arenaria macrophylla*, *Arnica latifolia*, *Artemesia douglasiana**, *Campanula scouleri*, *Claytonia spathulata* Dougl., *Corallorrhiza maculata*, *Dicentra formosa*, *Fragaria vesca* var. *bracteata*, *Hydrophyllum occidentale**, *Luzula spicata*, *Mitella diversifolia*, *Monardella odoratissima**, *Osmorhiza chilensis*, *Phacelia magellanica** Coville, *Polygonum phytolaceae* folium*, *Pyrola secunda*, *Rubus lasiococcus*, *Senecio triangulatus**, *Smilacina stellata* (L.) Desf.

12. Species of forests of high elevations, centered above 1800 m, character-species of subalpine forests dominated by *Tsuga mertensiana* and *Abies nobilis*, and species of both these forests and more open situations (*): Trees—*Abies nobilis*, *Tsuga mertensiana*. Shrub—*Lonicera conjugalis**. Herbs—*Anemone quinquefolia*, *Angelica arguta*, *Aquilegia formosa**, *Aster siskiyouensis*, *Bromus carinatus**, *Carex rossii*, *C. tracyi**, *Castilleja miniata**, *Claytonia parvifolia* Moe., *Corallorrhiza mertensiana*, *Delphinium sonnei* Greene, *Elymus glaucus**, *Epilobium hornemannii*, *Erigeron aliceae**, *Erysimum capitatum** (Dougl.) Greene, *Ligusticum grayi**, *Lupinus albicaulis**, *Mertensia bella*, *Mitella breweri*, *Orogenia fusiformis*, *Pedicularis racemosa*, *Penstemon anguineus*, *P. nemorosus*, *P. newberryi* Gray, *Poa bolanderi**, *Polygonum davisiae**, *Sanicula nevadensis**, *Saxifraga ferruginea*, *Smilacina racemosa* var. *glabra*, *Trisetum spicatum*, *Valeriana sitchensis* ssp. *sitchensis*, *Veratrum insolitum**, *Viola praemorsa*, *V. sheltonii*.

13. Parent-material ubiquitists, occurring at low elevations on diorite, gabbro, and serpentine: Trees—*Chamaecyparis lawsoniana*, *Pinus lambertiana*, *Pseudotsuga menziesii*. Herbs—*Adiantum pedatum* var. *aleuticum*, *Chimaphila umbellata* var. *occidentalis*, *Disporum hookeri*, *Festuca ovina*, *Luzula campestris*, *Smilacina racemosa*, *Trientalis latifolia*, *Trisetum canescens*, *Whipplea modesta*.

14. Elevation ubiquitists, occurring in forests of all elevations on diorite: Herbs—*Campanula scouleri*, *Chimaphila menziesii*, *Chimaphila umbellata* var. *occidentalis*, *Festuca occidentalis*, *Hieracium albiflorum*, *Melica subulata*, *Phlox adsurgens*, *Pyrola picta*, *Smilacina racemosa*, *Trillium ovatum*.

VI. FLORISTIC COMPARISONS

Floristic comparisons for different vegetation patterns and communities in the Siskiyou Mountains are summarized in three tables (17, 18, 20). These tables are intended to show the manner in which life-form composition, growth-form composition and species-diversities, and geographic relations of floras

change in relation to four major environmental gradients—the diorite-gabbro-serpentine series of parent materials, local topographic moisture gradients on each of these, elevation on diorite, and the east-west climatic gradient. The basic unit of comparison is the transect flora—the list of species (with presence values of 4% or more) in a given transect of 50 samples. One list (1920-2140 m on diorite) included all species in a 16-sample transect; and the lists for the east-west climatic gradient are based on all species of 6-sample transects. The comparisons for different moisture-gradient conditions and community-types in the central Siskiyous are based on lists of species occurring more than once in the mesic, intermediate, and xeric ranges of the transects (steps 1-2, 3-7, 8-10). The lists for mesic, intermediate, and xeric sites correspond to community-types: on diorite—Chamaecyparis-Pseudotsuga, Pseudotsuga-sclerophyll, and sclerophyll-Pseudotsuga forests; on gabbro—Chamaecyparis-Pseudotsuga, sclerophyll-Pseudotsuga, and Pinus-Pseudotsuga-Quercus-Arctostaphylos forests; on serpentine—Chamaecyparis-*P. monticola*-Pseudotsuga forest, mixed conifer stands with two-phase undergrowth (forest-shrub complex), Jeffrey pine woodland.

LIFE-FORMS AND GROWTH-FORMS

In the life-form spectra for lower elevations in the central Siskiyous (Table 17), floristic dominance is shared equally by phanerophytes and hemierythropophytes, with smaller, but substantial, numbers of chamaephytes and geophytes and few therophytes. These spectra represent the mixed evergreen forests and express the temperate, moderately humid forest climate of the region. Very similar spectra have been obtained for eastern deciduous forests, as represented in the spectra for Appalachian cove forest (mixed mesophytic) and Long Island oak-chestnut forest in Table 17. The spectra give no indication of the wide differences in climate and physiognomy of these forests on opposite sides of the continent; life-form spectra are relatively insensitive to some differences of environment and community character, highly sensitive to others. The "normal spectrum" for the flora of the world computed by Raunkiaer (1918, 1934) is often used as a standard of comparison. For detailed comparisons among temperate-zone forests a different kind of standard may be appropriate—one representing mesophytic, floristically rich forests of unglaciated areas, midway between the phanerophyte dominance of the tropics and warm-temperate forests and the hemierythropophyte dominance of cooler-temperate forests. The very similar spectra for Arcto-Tertiary remnants on opposite sides of North America suggest such a spectrum. Averaging two spectra for the Mixed Mesophytic Forest of the East (Withrow 1932, Cain 1945) and two for the Mixed Evergreen Forest in the West (South Fork and Beaver Creek, for the transition to redwood forest and a more continental phase) gives the gen-

TABLE 17. Relations of life-forms to environments in the Siskiyou Mountains, per cents of species in floras of transects and site groupings.

	Phanerophytes	Chamaephytes	Hemicryptophytes	Geophytes	Therophytes	No. of species
A. Central Siskiyou Mtns., by parent materials, 610-915m						
Quartz diorite.....	32	12	30	24	2	84
Olivine gabbro.....	32	14	32	19	2	101
Serpentine.....	20	19	44	15	3	116
B. Central Siskiyou Mtns., by sites, 610-915m						
On diorite—Mesic.....	35	14	28	21	2	72
Intermediate.....	33	10	33	22	2	79
Xeric.....	31	8	42	13	6	47
On gabbro—Mesic.....	34	11	33	21	1	74
Intermediate.....	30	22	35	12	1	72
Xeric.....	29	23	38	8	2	66
On serpentine—Mesic.....	27	19	35	18	1	88
Intermediate.....	25	24	39	12	1	102
Xeric.....	15	17	43	14	11	76
C. Central Siskiyou Mtns., by elevation belts on diorite						
460-760 m.....	35	10	32	19	3	86
760-1070 m.....	33	12	33	20	3	92
1070-1370 m.....	30	9	37	20	4	99
1370-1680 m.....	25	10	40	21	4	106
1680-1920 m.....	18	14	44	18	6	98
1920-2140 m.....	10	17	54	12	7	72
D. West-East climatic gradient across Siskiyou, low elevations						
Mill Creek.....	48	5	34	13	0	41
South Fork.....	38	10	29	23	0	58
Siskiyou Fork.....	40	9	31	20	0	56
Sturgis Creek.....	33	12	37	16	2	93
Beaver Creek.....	30	14	37	15	4	102
Emigrant Creek.....	27	5	35	10	23	81
E. Comparable spectra from other areas						
Cove forest, Great Smoky Mts., Tenn. (Cain 1945).....	36	4	30	26	3	113
Mixed mesophytic forest, Cincinnati, Ohio (Withrow 1932).....	34	4	34	23	4	127
Chestnut Oak forest, Long Island, N.Y. (Cain 1936).....	35	11	33	21	1	92
Oak-hickory climax, Piedmont, N. Car. (Oosting 1942).....	60	0	36	4	0	89
Mediterranean live-oak forest, 0-500 m elev. (Braun-Blanquet 1936).....	54	9	24	9	4	
Beech forest, Cevenne Mts., 1000-1500 m elev. (Braun-Blanquet 1936).....	2	4	52	40	2	
Subalpine forests, Great Smoky Mts. (Cain 1945).....	21	2	57	17	3	301
Subalpine forests, Olympic Mts., Wash. (Jones 1936).....	12	7	49	31	1	
Subalpine forests, Mt. Rainier, Wash. (Jones 1938).....	11	8	47	31	3	
Serpentine and gabbro in Tuscani (Pichi-Sermolli 1948).....	11	9	40	15	26	405
"Normal spectrum" (Raunkiaer 1918, 1934).....	46	9	26	6	13	
Mid-temperate mesophytic forests.....	34	8	33	23	2	

eralized "mid-temperate mesophytic forest" spectrum entered in Table 17.

Effects of parent material within a given climate are indicated by the first three spectra of this table.

All three spectra have the general pattern of the mixed evergreen forests; but from diorite through gabbro to serpentine the phanerophytes and geophytes decrease, while chamaephytes and hemicyrptophytes increase. The effect of the topographic moisture gradient at low elevations on diorite, as represented in the second series of spectra, appears in reduction of chamaephytes, increase in hemicyrptophytes and therophytes toward drier sites. Somewhat comparable results appear in the contrast of north and south-facing slopes within the same climate in the eastern forests by Oosting (1942), Cantlon (1953), and Miller & Buell (1956). Generally similar trends in relation to site moisture appear also in the low-elevation gabbro and serpentine floras. The xeric serpentine spectrum, representing Jeffrey pine woodland, is the lowest in phanerophytes of the low-elevation Siskiyou forests, and is similar in character to the spectrum for ophiolitic soils (serpentines and gabbros) in a drier Mediterranean climate as given by Pichi-Sermolli (1948, see Table 17). Changes in life-form representation with elevation in mountains, such as have been shown in other areas by Guyot (1920), Hansen (1930), Raunkiaer (1934), Gelting (1934), Braun-Blanquet (1936, see Table 17), Jones (1936, 1938), Allan (1937), Davidsson (1946), Cain (1950), Dansereau (1957), and Costin (1959), are indicated in the third series of spectra. The decline of the phanerophytes and increase of the chamaephytes and hemicyrptophytes toward higher elevations are consistent with observations in other areas; the slight increase in therophytes is in contrast to results in most other areas. The spectra for subalpine forests in the Siskiyous (1670-1920 and 1920-2140 m) resemble those of other subalpine or Canadian zone forests (Table 17) in proportions of phanerophytes and hemicyrptophytes, but differ in other respects. As suggested by the larger per cent of therophytes, subalpine climates in the Siskiyous are probably drier than in the other ranges.

The fourth series of spectra, finally, represent the change in climates from the coastal redwood forests at Mill Creek to the interior valley at Emigrant Creek; the central Siskiyou (Oregon Caves area) diorite sample fits into this series between Siskiyou Fork and Sturgis Creek. Since life-form spectra give little expression of the difference between maritime and continental climates, the gradient in question is primarily one of decreasing climatic humidity. The four gradients studied parallel one another to some extent in the kind of departure from the spectra of the mixed evergreen forests, or the generalized mid-temperate mesophytic forest, they produce. In this area an approach toward a more "extreme" environment, whether of parent material, elevation, or topographic or climatic dryness in almost all cases implies a decrease of phanerophytes and geophytes and an increase of therophytes.

Table 18 summarizes the distribution of growth-forms over some of the same range of environments. A number of trends in the representation of growth-

TABLE 18. Relations of growth-forms and species diversities to environments in the Siskiyou Mountains.

	Numbers of species in floras of transects and site groupings								Average number of species in vegetation samples		
	Trees	Shrubs	Forts	Graminoid	Total	% trees & shrubs	% evergreen	Trees	Shrubs	Forts	Graminoid
A. Central Siskiyou Mtns., by parent materials, 610-915 m											
Quartz diorite	17	13	46	8	84	43	7.9	4.0	10.7	0.9	23.5
Olivine gabbro	16	19	54	12	101	45	7.0	3.4	11.0	1.4	22.8
Serpentine	9	18	73	16	116	59	4.5	6.2	16.5	2.9	30.1
B. Central Siskiyou Mtns., by sites, 610-915 m											
On diorite—Mesic	15	11	42	4	72	42	9.7	4.5	11.7	0.7	26.6
Intermediate	15	11	48	5	79	50	7.6	3.9	11.0	1.2	23.7
Xeric	9	6	27	5	47	53	6.5	3.7	9.3	0.7	20.2
On gabbro—Mesic	16	10	40	7	73	41	7.0	4.0	10.7	0.8	22.1
Intermediate	10	13	44	5	72	52	7.0	2.8	9.9	1.5	21.2
Xeric	10	11	40	5	66	48	7.0	3.5	13.3	2.0	25.8
On serpentine—Mesic	9	18	56	5	88	59	5.3	8.3	18.4	2.2	34.2
Intermediate	9	19	68	6	102	72	5.2	6.6	16.8	2.5	31.1
Xeric	6	7	49	14	76	72	2.7	2.6	14.0	4.0	23.3
C. Central Siskiyou Mtns., by elevation belts on diorite											
460-760 m.	18	13	47	8	86	42	7.8	3.8	11.3	1.1	24.0
760-1070 m.	19	15	50	8	92	44	6.1	4.2	11.9	0.6	22.8
1070-1370 m.	15	12	62	10	99	55	3.8	4.4	20.2	1.0	29.4
1370-1680 m.	13	13	70	10	106	39	3.5	3.4	24.5	1.4	32.8
1680-1920 m.	6	8	76	8	98	36	2.5	1.7	18.4	1.7	24.3
1920-2140 m.	3	3	58	8	72	50	1.8	0.7	14.0	1.5	18.0
D. West-East climatic gradient across Siskiyous, low elevations											
Mill Creek	11	8	17	5	41	74	5.0	3.7	6.5	0.2	15.4
South Fork	11	11	33	3	58	46	5.2	5.0	8.6	0.7	19.5
Siskiyou Fork	13	10	30	3	56	57	7.3	5.0	9.4	0.3	22.0
Sturgis Creek	17	16	48	12	93	42	7.8	6.7	17.5	1.7	33.7
Beaver Creek	13	17	57	15	102	37	7.2	7.2	15.0	2.5	31.9
Emigrant Creek	10	12	44	15	81	33	4.2	3.8	12.0	3.7	23.7

forms in these floras are evident. Numbers of tree species may be observed to decrease (1) from diorite through gabbro to serpentine, (2) from low elevations toward higher ones, (3) from the central Siskiyous (Oregon Caves and Sturgis Creek) toward the Pacific Coast, (4) from the central Siskiyous toward the drier interior, and (5) from mesic sites toward xeric within the central Siskiyous. Numbers of shrub species (1) increase somewhat from diorite to gabbro and serpentine, (2) decrease toward higher elevations, (3) increase from the Coast to the eastern Siskiyous (Beaver and Sturgis Creeks), and (4) decrease from mesic sites toward xeric ones within the central Siskiyous. The decline in shrub species toward higher elevations parallels that for trees and is part of the very general decrease in floristic diversity of woody strata toward the north and toward higher elevations (cf. Whittaker 1956:11).

The increase in numbers of shrub species from the Coast toward the Interior is paralleled among the herbs. The data for Emigrant Creek suggest that these trends do not extend beyond the floristically rich communities of the eastern Siskiyous into those

of the continental Interior. Because of the disturbance at Emigrant Creek, however, the numbers of shrub and herb species there cannot be relied upon as comparable with those of the other transects. The increase in numbers of graminoid species along this same gradient into the drier and more open vegetation of the Interior is marked.

Within each of these growth-forms, trends in the representation of evergreen *vs.* deciduous forms appear, notably along the climatic gradient from the Coast inland. Evergreen forms are strongly dominant in all strata in the redwood forests at Mill Creek, they are predominant in the woody strata, at least, of the mixed evergreen forests of the central Siskiyous, but in the oak woodlands at Emigrant Creek deciduous forms are strongly dominant in all strata. The most striking expression of continentality in these floras is not in life-form spectra, but in the representation of evergreen forms both in numbers of species in floras and in community and stratal dominance.

SPECIES-DIVERSITIES

The data in Table 18 bear on another problem of community relations to environment—that of species-diversities, or the relative richness of communities in numbers of species. Studies of species-diversity (Fisher *et al.* 1943, Williams 1945, 1947, 1951, 1953, 1954, Preston 1948, Simpson 1949, Whittaker 1952, MacArthur 1957, Hairston 1959) have dealt mostly with animal populations, in which measurements can be based on numbers of species *vs.* numbers of individuals. Although measurements of this type can be applied to plants (Williams 1950, Margalef 1949, 1951, 1958, Black *et al.* 1950, Patrick *et al.* 1954, Hopkins 1955, Whittaker 1956, Dahl 1957, Curtis 1959) the author has preferred, because of the problem of what constitutes an individual among many plants, to deal with numbers of species in fixed sampling areas—whether the individual community-samples or the combined areas of the samples for a moisture-gradient transect.

There may be a general tendency for species-diversity, community productivity and biomass, development of the woody strata, and differentiation of the community into strata, to decrease from environments which are "favorable" in the sense of being warm, moist, and equable, toward environments which are "unfavorable" or "extreme" in their low temperatures, or aridity, or instability, or low nutrient levels, or high salinities. As indicated in Table 18, species-diversities do decrease along the moisture gradient in the mixed evergreen forests on diorite, and in a less clear-cut fashion on gabbro and serpentine. Species diversities increase, however, from the relatively humid and equable climates of the Coast toward the drier and more variable climates of the Interior. Even more striking is the increase in floristic diversity from the "normal" diorite to the "abnormal" serpentine soils. In relation to elevation, finally, it may be observed that the expected decrease in num-

bers of species toward higher elevations occurs among woody plants, but not herbs; and the diversity relations of the latter are such that total numbers of species increase into middle elevations before decreasing into the highest elevations sampled.

These data do not fit into any simple pattern of interpretation in relation to environmental favorableness. It is difficult to frame any definition of "favorableness" that does not amount to the observation that those environments are most favorable to high species-diversity where high species-diversities are encountered. Floristic diversity appears to occur as it occurs, a complex resultant of a number of influences which are at present scarcely understood. The limited interpretations which may be offered for the present material are as follows: (1) There is some correlation between species-diversity of a stratum and the extent of its development as expressed in coverage or biomass. This correlation, however, is conspicuously a partial one to which exceptions may be observed; one author (Yount 1956) has even suggested the reverse relation. (2) Diversity relations to environment are clearly different for different community fractions and groups of organisms (cf. Whittaker 1956:18). In the Siskiyous, a general inverse relation appears between diversities of tree strata and undergrowth. (3) In this vegetation the herb strata in all cases include half or more of the total vascular flora; and community diversity is in large part an expression of herb stratum diversity. (4) The conditions which are "favorable" for maximum diversity of herb strata, and thereby for community diversity, are not the conditions most favorable for development of the tree stratum and community biomass. Maximum herb-stratum diversities are encountered in the more open vegetations of drier climates and "atypical" parent materials, in which lower tree coverage permits greater development of the undergrowth. And, from low to middle elevations, herb-stratum and community diversity also increase as the density of tree cover (determined primarily by the density of sclerophylls) decreases.

Perhaps the most significant diversity trend encountered is that from maritime to continental climates. Average numbers of vascular plant species per sample increased inland from 15.4 in the Mill Creek redwood forests, to 33.7 in the mixed evergreen forests at Sturgis Creek. Biological meaning of this trend is quite uncertain. The greater variety of temporal niches, of life-history timings avoiding direct competition, in the more widely variable seasons of the continental climate may contribute to it, along with the more open structure of the inland forests. There is also a marked decrease in average amplitudes of species distributions along topographic moisture gradients, from the coast inland. The corollary of this decrease in species amplitudes is an increase in floristic differentiation of communities along the moisture gradient, from the coast inland. It is as if only one flora occupied the whole of the

moisture gradient in the redwood belt, but two or three floras in the inland environments. Because the distributions of species overlap more broadly in the maritime pattern, the community types there seem to intergrade and interpenetrate one another more broadly. Because of the narrower amplitudes in the continental climates, a larger number of distinguishable community-types appear along the moisture gradient, and these community-types seem more distinct.

The increasing species-diversities from the coast inland are thus the product of two phenomena—diversity of individual stands, and relative differentiation of vegetation patterns along topographic moisture gradients—, both increasing inland to produce the observed contrasts. The extent to which these contrasts characterize continental and maritime climates in general is unknown; but they are consistent with conditions of western Europe observed by Rübel (1927) and with the author's material on the central Siskiyous and the more strongly continental Great Smoky Mountains. The two phenomena involved suggest the need for distinguishing three aspects or levels of species-diversity in natural communities: (1) The richness in species of a particular stand or community, or a given stratum or group of organisms in a stand. Fisher's (1943) *alpha* index is one means of measuring this, which may be designated primary or "alpha" diversity. (2) The extent of change of community composition, or degree of community differentiation, in relation to a complex-gradient of environment, or a pattern of environments, which may be designated secondary or "beta" diversity. (3) The species-diversity of a number of community samples, for some range of environments, which have been combined, so that the diversity value is a resultant of both alpha and beta diversities of these samples. The transect diversities of Table 18 are of this tertiary or "gamma" diversity type, as are many of those for animal collections to which diversity measurements have been applied. The same types of measurements may be applied to "gamma" as to "alpha" diversity; "beta" diversity represents a different problem, to be discussed in the following section.

SAMPLE SIMILARITIES AND COENOCLINE DIFFERENTIATION

There are many possibilities for expressing the relative similarity or dissimilarity of two communities; but two most simple and direct ones have been most widely used—*coefficient of community* and *percentage similarity* (Whittaker & Fairbanks 1958). The coefficient of community, first used by Jaccard (1902a, 1902b, 1908, 1912, 1932; Koch 1957) is:

$$CC = \frac{\text{number of species in both samples or floras}}{\text{number of species in one or both}}$$

Percentage similarity, which, with variations, has been independently discovered and used by a num-

ber of authors (Gleason 1920, Kulczyński 1928, Renkonen 1938, Dyksterhuis 1949, Odum 1950, Whittaker 1952; Bray 1956, Curtis 1959) compares two samples in terms of percentage composition:

$$PS = 1 - 0.5 \Sigma |a - b| = \Sigma \min(a, b),$$

in which *a* and *b* are the percents which a particular species includes of the total samples A and B. The computation, and some of the limitations inherent in the measurement, have been discussed elsewhere (Whittaker 1952, Whittaker & Fairbanks 1958).

It has been observed that olivine gabbro is chemically intermediate to quartz diorite and serpentine, and correspondingly supports vegetation which is intermediate and connects the very anomalous serpentine communities with the "normal" ones of diorite. Physiognomically the gabbro vegetation is intermediate, but closer to that of diorite. It is consequently of interest to determine the underlying floristic similarities of these vegetation patterns, computing coefficients of community for lists of 81, 101, and 116 species in the transects. Resulting values were—diorite *vs.* gabbro 34.4%, gabbro *vs.* serpentine 38.2%, diorite *vs.* serpentine, 14.8%. The gabbro flora shares species in almost equal proportions with diorite and serpentine.

Percentage similarities also were used to compare the three vegetations in terms of quantitative composition of stands. The three comparison standards (see Part II) for mesic sites (ravines), intermediate slopes (open E-facing), and xeric slopes (open SW-facing) were compared in all possible combinations, with separate computations for the tree strata and undergrowth. Relations of interest in the resulting sample-association matrices include the following:

1) In general, the gabbro samples are clearly intermediate to the comparable samples from other parent materials; but in detail, complex interrelations appear. The gabbro ravine samples were more similar to serpentine than to diorite ravine sample in both strata; among E-slope samples gabbro was more similar to diorite than to serpentine; among SW-slope samples the gabbro undergrowth was equally similar to diorite and serpentine, but the tree stratum was closer to diorite. Averaging all three samples together, the undergrowth of gabbro was closer to serpentine (21%) than to diorite (15%), while the tree stratum of gabbro was closer to diorite (36%) than to serpentine (20%).

2) In general, the contrast between the different vegetation patterns increased from mesic sites to xeric ones. Averaging percentage similarities for the strata and parent materials (diorite *vs.* gabbro and gabbro *vs.* serpentine) gave: 30% for ravine samples, 27% for east slopes, and 13% for southwest slopes.

3) In all cases the SW-slope samples were more similar to E-slope than SW-slope samples of the next parent material in the series—diorite, gabbro, serpentine. This fact is to be correlated with the "shift toward the mesic" of species distributions (Part VII).

4) Although percentage similarities for the tree stratum and undergrowth are necessarily correlated, lack of any strict consistency of these is evident in the data. In extreme cases contrasts of these values were as high as 67 and 34, 30 and 8, 9 and 1%. This fact is consistent with what has already been observed on the lack of strong correlation between different strata and community-fractions.

A further problem to which such measurements may be applied is that of degree of differentiation of the communities along an environmental gradient. "Half-changes" in a rather crude form were suggested in a previous study (Whittaker 1956) as a basis of such measurement. A quite different approach has been suggested as the "index of biotic dispersity" of Koch (1957).

The simplest measurement of beta diversity may be

the relation, $\beta = \frac{\gamma}{\alpha}$, in which α is the diversity value

for an individual sample and γ that for the sample resulting from merging a number of individual samples from a community pattern or coenocline. Thus, comparing Fisher *alpha* measurements for average numbers of tree species and individuals in individual samples, with those for tree species and individuals in whole transects, gives "beta" diversities of 1.95 for diorite, 2.24 for gabbro, and 2.33 for serpentine at low elevations, and 1.60 for high-elevation forests (1920-2140 m) on diorite. An alternative approach, when a particular gradient is in question, is direct comparison of the extremes of the gradient by either coefficient of community or percentage similarity. Results have been found generally unsatisfactory; for such values are often zeroes, or so low as to permit no effective comparison. In the search for a more effective measurement, a number of transects from the Great Smoky and Siskiyou Mountains have been studied to determine the relations of percentage similarity and coefficient of community to distance along ecological gradients.

When these values on a logarithmic scale are plotted against distance along a gradient, the curves take the form illustrated in Fig. 18. The striking feature of the curves is the apparent straight-line relation between environmental gradients and log of sample similarities along much of the length of the gradients. Three qualifications of this straight-line relation must, however, be observed: (1) These straight lines, extrapolated back to zero intervals along the gradient, strike the ordinate not at 100% but at 70% or 80% (and values as low as 40% and as high as 95% have been obtained on other transects). This is consistent with the fact that coefficient of community and percentage similarity measurements for two samples from the same stand yield not 100%, but values of these magnitudes (cf. Whittaker 1952:12 on "internal association," Bray & Curtis 1957). (2) Beyond a certain point, the lower parts of the curves slope off with rapidly increasing steepness toward zero similarity. This also must be

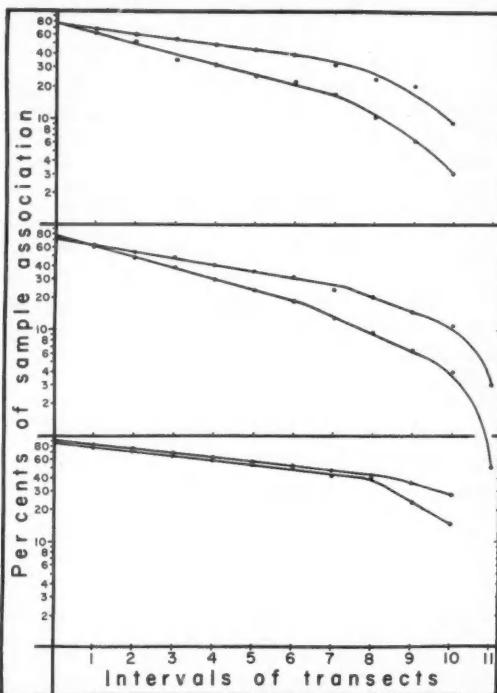


FIG. 18. Change in community composition, as measured by coefficients of community and percentage similarities for the tree strata, in relation to environmental gradients in transects. In each case the upper curve is for coefficients of community, the lower for percentage similarities; both these values are plotted on logarithmic scales. Top—along the elevation gradient in the Great Smoky Mountains; transect intervals are 400 ft (122 m). Middle—along the topographic moisture gradient between 460 and 760 m, Great Smoky Mountains. Bottom—along the topographic moisture gradient, 610-915 m on diorite, Siskiyou Mountains. Curves are smoothed by averaging values for given numbers of intervals along the transects; thus the first point plotted is an average of comparisons of samples one transect step apart, the second point an average of comparisons of transect steps two intervals apart, etc.

the case for, though species reach their limits gradually, one by one, along the gradient, a point is ultimately reached beyond which no species present in the first sample occurs. (3) In some curves of this type, steepness gradually increases beyond the first 2-3 intervals of the transect.

For the straight portions of the curves, change in community composition in relation to distance along an environmental gradient may be expressed in relatively simple form: $y = ab^x$, in which y is sample similarity (coefficient of community or percentage similarity), x is the number of intervals along the gradient, a is the value of y for zero distance, and b is the constant ratio which determines the slope of the line on log-linear plot and expresses rate of com-

munity change in relation to the scale of the x axis.

Or: $y = ae^{-\lambda x}$, in which λ also is a constant for slope in the form of the decay constant. This relation may provide, with due allowance for its limitations, a unit for "ecological distance" (Whittaker 1952, 1956)—relative distance along an environmental gradient, as expressed in change in community composition in response to that gradient. The "half-change" unit may be defined as the distance along an environmental gradient necessary to reduce sample similarity to one-half that of the zero distance.

When coefficient of community or percentage similarity values are available for a transect, the number of half-changes along the gradient may be determined:

$$z = a \times 2^{-\beta}$$

$$\beta = \frac{\log a - \log z}{\log 2}$$

in which β is the number of half-changes, a is the sample similarity at zero intervals, and z is the sample similarity for samples from the extremes. This measurement, however, gives a disproportionate weight to the sample comparison for the extremes. A measurement which better expresses community change along the gradient as a whole can be derived from the slope of the first, nearly linear portion of the curve. The line formed by this, extrapolated to the number of environmental intervals represented by the extremes of the transect, indicates a value of z , from which a value for β may be determined. Table 19 gives percentage similarity half-changes by both methods. From this, and the author's other ma-

TABLE 19. Change in community composition (percentage similarities) along the topographic moisture gradient in low-elevation transects in the Siskiyou Mountains, by parent materials and strata.

Transect	Estimated percentage similarity for zero transect steps	Percentage similarity for transect steps 1 and 10	Indicated half-changes	Percentage similarity of transect steps 1 & 10 from extrapolation of straight line	Indicated half-changes
Diorite					
Trees.....	90	17.8	2.5	43	1.1
Shrubs.....	90	14.2	2.7	22	2.0
Herbs.....	82	5.8	3.7	15	2.4
Gabbro					
Trees.....	73	27.9	1.4	40	.86
Shrubs.....	72	25.0	1.5	38	.92
Herbs.....	70	14.3	2.3	24	1.6
Serpentine					
Trees.....	80	7.0	3.5	23	1.8
Shrubs.....	72	7.0	3.4	21	1.8
Herbs.....	70	3.8	4.2	18	2.0

terial on the Great Smoky and Siskiyou Mountains, the following observations are suggested:

1) Extent of change of community composition, or "coenocline differentiation," as measured in half-changes along the moisture gradient, increases from the diorite to the serpentine vegetation pattern. The lower coenocline differentiation on gabbro may reflect its location closer to the coast.

2) Extent of population change along the moisture gradient tends to increase from the tree, through the shrub, to the herb stratum (Table 19). This contrast in rates of change of different strata becomes conspicuous in some subalpine forests (Whittaker 1956).

3) There is some decrease in coenocline differentiation with increasing elevation in the forest vegetation of the Smokies and the central Siskiyous. This tendency does not apply equally to all strata and elevations, and is most marked in the tree strata of highest elevations.

4) There is a very impressive increase in coenocline differentiation in all strata from the Coast inland in the Siskiyous, as indicated above. Coenocline differentiation is still higher in the lower-elevation forests of the Great Smoky Mountains, in a more continental climate, than in any of the mixed evergreen forest areas.

5) Coenocline differentiation and numbers of species in individual stands, beta and alpha diversities, appear to increase and decrease in parallel over most of the range of environments represented in the study.

The results discussed do not fit into any very simple pattern of interpretation. The greater humidity and more equable temperatures of the maritime climate may imply smaller contrast of moisture-balance conditions in most xeric and most mesic sites, and therefore a smaller contrast of moisture-balance conditions along the topographic moisture gradient in a maritime, as compared with a continental, climate. The more open vegetation structure of serpentine, with greater exposure to insolation and evaporation, may imply greater contrast in moisture-balance conditions along the moisture gradient than on diorite.

In general, extent of change in community composition seems correlated with extent of environmental contrast along the topographic moisture gradient. Coenocline differentiation is not a direct expression of range of environments, however. In the Great Smoky Mountains there is striking contrast in the degree of change in tree-stratum composition between the *Picea-Abies* forests above 4500 feet on the one hand, and the mostly deciduous forests outside the range of spruce and fir at the same elevations, on the other. Coenocline differentiation may thus be affected by the kinds of communities that develop in a range of environments, as well as by that range of environments itself. Coenocline differentiation, like species-diversity of samples, is presumably a community characteristic complexly related to characteristics of environments and of the communities which

TABLE 20. Geographic Relations of Floras.

	PARENT MATERIAL AND ELEVATION IN THE CENTRAL SISKIYOU MTS.							EAST-WEST CLIMATIC TRANSECT OF THE SISKIYOU MTS. AT LOW ELEVATIONS					
	Low-Elevation Forests			High-Elev. Forests		Summits		West. Coastal			East. Continental		
	Quartz diorite	Olivine gabbro	Serpentine	Quartz diorite	Serpentine	Quartz diorite	Serpentine	Mill Creek	South Fork	Siskiyou Fork	Sturgis Creek	Beaver Creek	Emigrant Creek
Total nos. of spp. in transect floras.....	84	101	116	81	87	54	48	41	58	56	93	102	81
Floristic Groups (per cent of transect floras)													
Siskiyou Endemic.....	1	7	16	4	5	2	8	2	2	2	1	3	
Klamath Endemic.....		3	9	6	7	10			2	1	8	6	
Sierran.....	4	9	10	6	10	7	6	2	3	2	3	8	6
Sierra-Cascadian.....	8	5	3	7	2	7	2		7	9	6	5	6
Cascadian.....	1		1	6	5	6	6	2	2	2	1	3	
Sierra-Coastal.....	6	13	9	1	7	4	2	2	3	5	6	5	4
Coastal.....	12	20	15	6	11	6	6	7	9	11	11	10	5
Coastal-Northern.....	17	9	5	6	2	2		39	28	27	12	11	7
Western.....	36	25	21	38	34	46	48	27	34	30	39	37	48
Nearctic.....	15	10	11	25	17	13	10	17	10	12	19	19	23
Floristic Vectors													
Tree: North.....	3.4	3.1	3.0	4.2	2.9			3.6	3.5	3.3	3.4	3.5	4.0
East.....	2.3	2.3	2.3	2.8	2.7			2.4	2.4	2.2	2.5	2.9	2.8
South.....	3.0	3.4	3.3	2.2	3.4			2.2	3.0	2.8	3.2	3.5	3.8
Total.....	8.7	8.8	8.6	9.2	9.0			8.2	8.9	8.3	9.1	9.9	10.6
Shrub: North.....	3.7	2.6	1.5	3.0	2.2	3.0		4.1	4.6	4.0	3.2	3.4	3.2
East.....	2.5	2.0	1.6	2.8	2.5	2.8		1.8	2.5	2.4	2.6	2.8	3.2
South.....	2.6	2.6	2.1	2.0	3.3	3.0		2.4	2.5	2.7	2.7	2.6	3.2
Total.....	8.8	7.2	5.2	7.8	8.0	8.8		8.3	9.6	9.1	8.5	8.8	9.6
Forb: North.....	3.6	2.5	1.9	3.6	2.5	2.8	2.1	4.3	3.6	3.8	3.4	3.2	3.4
East.....	2.9	2.2	1.9	3.4	3.0	3.0	2.7	3.2	2.8	3.0	3.2	3.2	3.2
South.....	2.8	2.5	1.8	2.5	2.3	2.4	2.0	3.1	2.9	2.9	2.8	2.5	3.0
Total.....	9.3	7.2	5.6	9.5	7.8	8.2	6.8	10.6	9.3	9.7	9.4	8.9	9.6
Graminoid: North.....	4.4	3.4	3.3	4.6	4.1	3.5	3.6	4.6	4.0	3.3	4.0	4.5	4.2
East.....	4.2	3.3	3.8	4.6	4.4	3.8	4.1	2.8	2.3	3.3	5.1	4.6	4.9
South.....	2.9	2.6	2.9	3.2	3.1	3.5	3.4	2.0	2.3	2.7	3.1	2.7	2.8
Total.....	11.5	9.3	10.0	12.4	11.6	10.8	11.1	9.4	8.6	9.3	12.2	11.8	11.9
All together: North.....	3.6	2.7	2.1	3.8	2.7	2.9	2.3	4.1	3.8	3.8	3.5	3.5	3.6
East.....	2.8	2.3	2.2	3.5	3.1	3.1	2.9	2.7	2.6	2.7	3.2	3.3	3.5
South.....	2.8	2.7	2.1	2.6	2.6	2.6	2.3	2.6	2.8	2.8	2.9	2.7	3.1
Total.....	9.2	7.7	6.4	9.9	8.4	8.6	7.5	9.4	9.2	9.3	9.6	9.5	10.2
Maximum extents (per cent of transect floras)													
North.....	45	29	21	37	22	22	10	56	47	45	34	33	30
East.....	13	10	15	23	22	22	25	17	9	12	20	18	18
South.....	13	27	23	9	20	19	12	12	12	14	16	12	15
Indeterminate	29	35	41	31	37	37	52	15	33	29	30	37	37

develop in those environments, and may be very differently expressed in different strata and groups of organisms in the same communities.

GEOGRAPHIC RELATIONS OF FLORAS

Another approach to analysis of relations of plant life to environments in the Siskiyou Mountains is possible, that dealing with geographic relations of floras. The comparisons given in Table 20 are based on transect floras; data are given also for species in 6 samples of high-elevation serpentine vegetation ranging from *Abies nobilis* forest to *Pinus jeffreyi* woodland at elevations between 1900 and 2100 m on Big Red and Little Red Mountains and Observation Peak. Summit lists are based on collections from

four of the high peaks on acid or intermediate rocks (Lake Mtn., Mt. Elijah, and Grayback Peak, and Mt. Ashland) and two high peaks of serpentine (Big Red Mtn. and Observation Peak).

Geographic relations of all species, and subspecies and varieties, were codified in two ways. All were classified first by areal types on the basis of statements of distribution in floristic manuals (primarily Peck 1941, Abrams 1940-51, Jepson 1923-5). Areal types in relation to plant communities have been much less studied in North America than in Europe (cf. Hansen 1930, Böcher 1938, 1954, Meusel 1939, 1943, Schmid 1950, Ellenberg 1950, Walter 1954), and the information on which to base them is less adequate; but a system was developed with the fol-

lowing major types: (1) Siskiyou Endemics—species (or, when distinguished, subspecies or varieties) restricted to the narrower area of the Siskiyou Mountains, (2) Klamath Endemics—restricted to the larger Klamath Region, (3) Sierran—extending south from the Klamath Mountains and having the principal area of occurrence in the Sierra Nevada, (4) Cascadian—extending northward and having the principal area of occurrence in the Cascade Range, (5) Sierra-Cascadian—extending both north into the Cascades and south into the Sierra Nevada, (6) Sierra-Coastal—extending south from the Klamath Region both in the Sierra Nevada and the Coast Ranges, (7) Coastal—extending along the California and Oregon coasts (including coastal mountains), but not north along the coast to Washington, (8) Coastal-Northern—extending northward along the coast to Washington and beyond with extensive occurrence in the area of mesophytic forests surrounding Puget Sound, (9) Western—widespread in the western Interior, especially the Great Basin and interior mountain ranges, (10) Nearctic—of wide distribution in North America, extending eastward beyond the Rocky Mountains.

The second approach was through actual extent of species areas in a given direction—north (and west to Alaska), east, and south. Because of the difficulty of translating statements of distribution in floristic manuals into numbers of km, arbitrary 7-point scales were used to express distances of extent, not beyond: 0—the Siskiyou Mountains themselves in a given direction; 1—the Klamath Region north and south, and the Cascades east; 2—the Oregon-Washington border northward, the Oregon-Idaho border and central Nevada eastward, and middle California (Monterey) southward; 3—the Washington-British Columbia border northward, the Idaho-Wyoming border and central Utah eastward, and southern California (Los Angeles) southward; 4—Prince Rupert, British Columbia northward, eastern Wyoming and the Colorado Front Range eastward, northern Baja California southward; 5—the north-south border of Alaska and Yukon territory and its projection to the coast northwestward, west-central Kansas and Nebraska (100th meridian) eastward, Guaymas southward; 6—the Alaska Peninsula and Bering Sea northwestward, the Mississippi River eastward, Mexico City southward; 7—northwestward into Siberia, eastward to the Atlantic Ocean, southward into Central America or beyond.

Representation of areal types in the low-elevation floras of the three parent materials in Table 20 is very significantly different. There are few narrowly endemic species in the diorite flora (*Tauschia kelloggii* is the only such species in the list); but the number of species endemic to the Siskiyou Mountains and the Klamath Region increases to 10% of the gabbro and 25% of the serpentine floras. The three parent materials show marked differences also in the decreasing representation of Coastal-Northern species and increasing importance of a southern or "Californian"

grouping including the Sierran, Coastal, and Sierra-Coastal species from diorite to serpentine. These relations seem interpretable on the basis that the gabbro and serpentine vegetation is more open and more xerophytic in appearance, with greater exposure of the undergrowth to light and evaporation. A larger proportion of the species of the closed forests on diorite extend into the relatively dense mesophytic forests to the north of the Siskiyous; a larger proportion of the gabbro and serpentine floras extend into the more open and xerophytic communities of California (Whittaker 1954b). The data suggest that different parent materials in the same climate may not only have marked effects on extent of narrow endemism in their floras, but may act as differential filters, admitting different proportions of species from the whole spectrum of geographic relations into their floras.

Various trends in floristic relations appear when floras of low-elevation forests on diorite and serpentine are compared with those of high-elevation forests and high summits on these same parent materials. The proportion of narrow endemics is higher in the higher-elevation floras on diorite, and representation of wide-spread Western species (of interior mountains, primarily) increases toward higher elevations, especially on serpentine. The contrast between serpentine and diorite floras decreases toward higher elevations, though it is by no means absent at the highest elevations available for study. This trend is consistent with the more general observation that floristic distinctiveness of serpentine is less in far-northern environments (and especially glaciated areas) than in warm-temperate and tropical ones (Whittaker 1954b).

Floristic trends in the east-west climatic transect include: (1) Decreasing proportions of coastal species, in the broad sense, toward the interior. (2) Among the different coastal groups, the Coastal-Northern species decline in numbers into the drier climates of the interior, but the Coastal and Sierra-Coastal species increase in numbers from Mill Creek to Sturgis Creek. There is no paradox in this increase of "Coastal" species toward the interior since most of them are species of the California Coast Range mountains, rather than the more narrowly maritime environments of the coast itself. (3) Representation of Sierran and Sierra-Cascadian species increases toward the interior. (4) Representation of the widespread Western and Nearctic species also increases inland. These trends seem clearly correlated with climates; for the more mesophytic species of the Coastal-Northern grouping decrease toward the interior while species of the somewhat drier and more continental climates of the California mountains and the interior increase. Representation of narrowly endemic species is small throughout; for representation of these is generally high on special parent materials, moderate at high elevations on any parent material, but low on the more "normal" parent materials at low elevations.

The data on floristic "vectors," or relative extents in different directions, are compiled in two forms in Table 20. Distance values for the different directions have been averaged for species within growth-forms, and for whole floras; and numbers of species with greatest extent in a given direction, according to the scale values, are tabulated also for whole floras. Direction of greatest extent is determined in this case by the largest of the three values for directional extent. "Indeterminate" species are those in which the two highest scale values were equal; and many of the narrow endemics are included among these.

A very marked decrease in average extent of species areas appears in the series of floras from diorite through gabbro to serpentine. This decrease applies, in essentially parallel fashion, to the shrub and forb groupings; but it does not apply to trees and graminoids; for the conifers and grasses of serpentine are predominantly widespread Western or Nearctic species. In directions of maximum extent also, the diorite and serpentine floras are in contrast. A high proportion of species have maximum extent to the north in the former, maximum extent to the south in the latter. On both soils average distances of extent appear to increase from low-elevation into high-elevation forests, but to be lower in the summit floras with their greater representation of alpine endemics, than in the high-elevation forests.

Other approaches to floristic generalization were experimented with. Correlations of geographic relations and topographic moisture gradients were studied. On diorite and gabbro some correlation in the expected direction appeared; average extents toward the north were greater, and a higher proportion of species had maximum extents toward the north, in mesic sites than in xeric. No such correlation was observed in the more strongly endemic serpentine flora. Analysis of dispersion values for the distances of extent, as an approach toward measurement of relative floristic heterogeneity, was attempted. No significant differences were obtained, apart from those resulting from degree of endemism. Measurements of relative difference in extent to the north and the south were attempted as an approach to measurement of the degree to which the different floras were intraneous or extraneous to the Klamath area. Again, no significant differences appeared which did not result from the proportion of narrow endemics. These and other approaches to floristic abstraction encounter a fundamental limitation in the fact that all floras are mixtures of species with heterogeneous, "individualistic" relations to climate and geography. Yet the different communities within a limited area do differ significantly in geographic relations of their floras; and these differences are systematic and interpretable, and subject to measurement.

VII. RELATIONS OF SPECIES POPULATIONS TO THE THREE SOILS

The results of the study which remain to be discussed are autecological—the manner in which species

populations are distributed in relation to the three soils.

TREES

Pseudotsuga menziesii is the major tree species of low elevations; and on all three soils it extends along most or all of the moisture gradient with apparently bimodal populations (Fig. 20). Average densities of *Pseudotsuga* stems are considerably lower on gabbro and serpentine; densities of stems from the 1-in. class up per hectare were 177, 60, and 78 on the three soils. Effects of serpentine and gabbro are more striking when numbers of large stems are compared; densities of stems 37 cm (15 in.) dbh and over on the three soils were 88, 19, and 23. The ratio between the two density values, expressed as numbers of stems 37 cm and over among 100 stems over 1 cm dbh, provides an indication of slope of the stem number-diameter curve (Part IV), and average survival of trees into larger size classes. These values for diorite, gabbro, and serpentine were 49.7, 32.6, and 6.0, indicating an appreciable reduction of average *Pseudotsuga* size on gabbro, as compared with diorite, and a striking reduction on serpentine. Increment borings are available for diorite and serpentine; the lower rate of diameter growth on the latter is illustrated in Fig. 19 (see also Fig. 14).

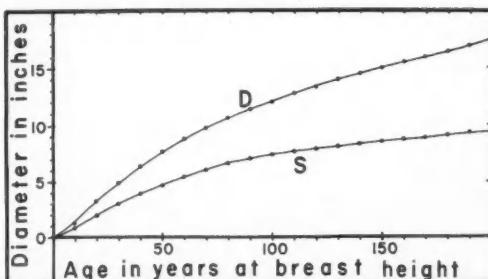


FIG. 19. Growth in diameter in relation to age for *Pseudotsuga menziesii* on diorite (D) and serpentine (S), based on 11 increment borings for low elevations on diorite, 7 increment borings from serpentine, chosen to represent all sites and average out site differences on a given parent material.

Chamaecyparis lawsoniana was of about equal abundance on diorite and serpentine but less abundant in the gabbro transect. The reduction in tree size on serpentine which is so evident in *Pseudotsuga* did not appear in *Chamaecyparis*, which is in consequence a smaller tree than *Pseudotsuga* on diorite, but a larger one on serpentine. Whereas the densities of *Pseudotsuga* and *Chamaecyparis* were lowest in the gabbro transect, that of *Pinus lambertiana* was highest there. Relative survivals into larger size classes were similar on all three soils, but *P. lambertiana* showed very different relations to the moisture gradient on the different soils (Fig. 20). On diorite the population is highest in xeric sites, on gabbro in subxeric ones (significance of the mesic population peak is doubt-

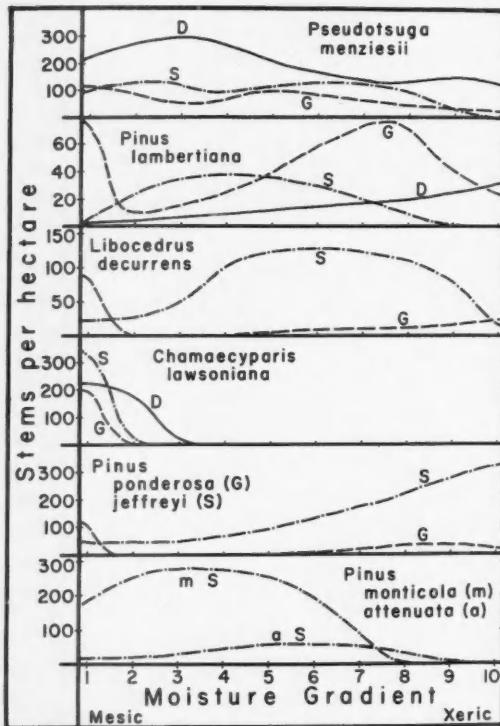


FIG. 20. Population distributions of conifers in relation to topographic moisture gradients at low elevations on diorite (D), gabbro (G), and serpentine (S). In this and following figures, populations on diorite are represented by continuous lines, those on gabbro by broken lines, and those on serpentine by dot-and-dash lines.

ful), on serpentine in submesic ones. Through the series of soils the population center or mode is displaced progressively toward the mesic end of the gradient. Such "shifts toward the mesic," as they will be called, are a most general feature of the population relations to be discussed.

Among the sclerophyllous trees, both *Lithocarpus densiflora* and *Quercus chrysolepis* have apparently bimodal populations on both diorite and gabbro (Fig. 21). Both species are represented on serpentine by shrubby varieties with submesic modes (*Lithocarpus densiflora* var. *echinoides* and *Quercus chrysolepis* var. *vaccinifolia*). *Castanopsis chrysophylla* occurs on diorite with a large and apparently bimodal population; its occurrence on the other soils is scattered and irregular, but the serpentine population again is predominantly shrubby (*Castanopsis chrysophylla* var. *minor*). *Arbutus menziesii* occurs on diorite, with an apparently bimodal population centered in more xeric sites, and on gabbro with a lower population centered in submesic sites; there is no shrubby form on serpentine, where the species is represented by trees of uncommon and irregular occurrence. *Umbellularia*

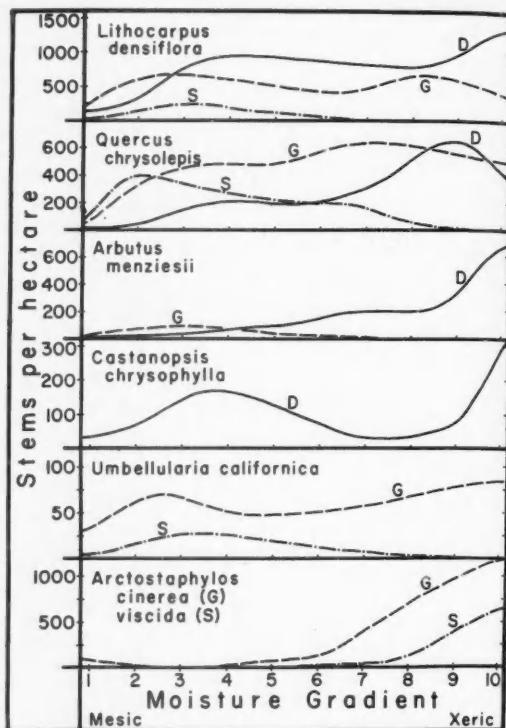


FIG. 21. Population distributions of sclerophylls on diorite (D), gabbro (G), and serpentine (S).

californica is almost absent from diorite; it is an abundant small tree on gabbro and a common shrub, with habitus very different from that on gabbro, on serpentine.

UNDERGROWTH SPECIES

Figs. 22-25 summarize distributional relations for a number of major undergrowth species. Almost all show the shift toward the mesic, though there are a few exceptions (e.g. *Whipplea modesta* from diorite to gabbro, Fig. 23) presumably implying occurrence of ecotypic populations with greater drought tolerance on the more mafic soils. In some undergrowth species, as in a number of trees, there is evidence of genetic complexity in population bimodality along the moisture gradient. The last four species, in Fig. 25, are bimodal in relation to the parent-material gradient, with higher populations on diorite and serpentine, lower on the intermediate gabbro.

Further complexities appear in *Polystichum munitum* and *Trientalis latifolia* (Figs. 23 and 25). *P. munitum* var. *munitum* is an important mesic population on diorite, with an apparent secondary mode in subxeric sites. The population on gabbro (predominantly var. *imbricans*) is centered in submesic sites; allowing for the shift toward the mesic this may correspond to the subxeric-xeric population on diorite (in which var. *imbricans* or its characteristics appear

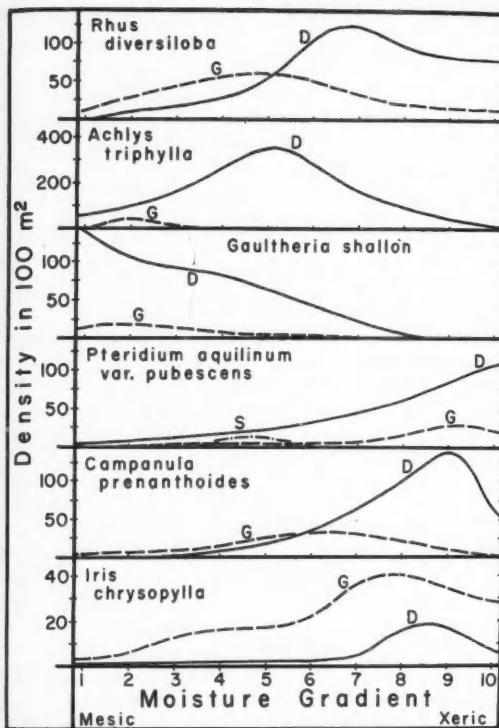


FIG. 22. Population distributions of undergrowth species on diorite (D) and gabbro (G).

exceptionally). Only var. *imbricans* appears on serpentine, with a shift toward the mesic compared with the gabbro population. *Trientalis*, with two modes in relation to moisture on diorite and a third on serpentine, has a triangular pattern of population centers in relation to the moisture and parent-material gradients. *Trientalis* is also one of a number of undergrowth species (*Rosa gymnocarpa*, *Symporicarpus rivularis*, *Whipplea modesta*, *Apocynum pubescens*, *Smilacina racemosa*, *Senecio bolanderi*) showing evidence of population bimodality in relation to elevation (Tables 13 and 14).

GENERAL RESULTS

The shift toward the mesic is one of the general features emerging from such study: In general, a species population which is observed on two or more soils of the diorite-gabbro-serpentine series in the same climate, will show a shift of its population distribution toward more mesic sites on the more mafic soil. Comparable shifts in relation to climate are more familiar. In transects of different elevation belts on diorite, high-elevation species shift toward the mesic as their populations are followed down into the warmer and drier climates of lower elevations; and low-elevation species show parallel shifts toward the xeric toward higher elevations. Shifts of the same

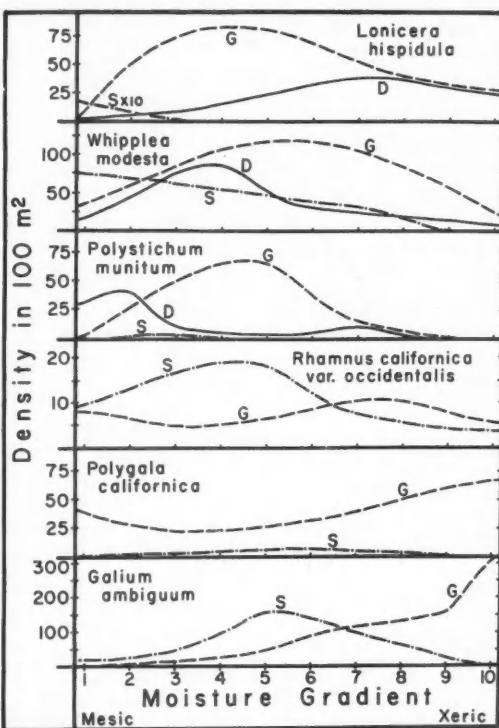


FIG. 23. Population distributions of undergrowth species on diorite (D), gabbro (G), and serpentine (S).

nature are observed along the east-west gradient from humid to drier climates (Part IV). The interrelation of local topographic and broader climatic distributions of species, with the tendency of topographic distributions to shift in such a manner as to compensate for differences in climate, has twice been formulated as a distributional "law"—the law of geo-ecological distribution of Boyko (1945, 1947) and the law of relative site constancy of Walter & Walter (1953).

The three parent materials studied are in similar general climates. To the extent that the shift may represent a response to climate, it is a response not to general climate outside communities, but to microclimates within communities as affected by the kinds of vegetation developing on the three soils. Equivalence of moisture-balance conditions in such different ecosystems, with different relations between soil moisture and evaporative conditions, as these three soils may be very difficult to define. The average magnitudes of the shifts toward the mesic, measured in terms of steps of the ten-step transects, may indicate something of what equivalent moisture-balance conditions on the three soils are. Among sets of 8 species which could be compared on two of the three soils, the average shift toward the mesic was 3.0 transect steps from diorite to gabbro, 4.2 transect

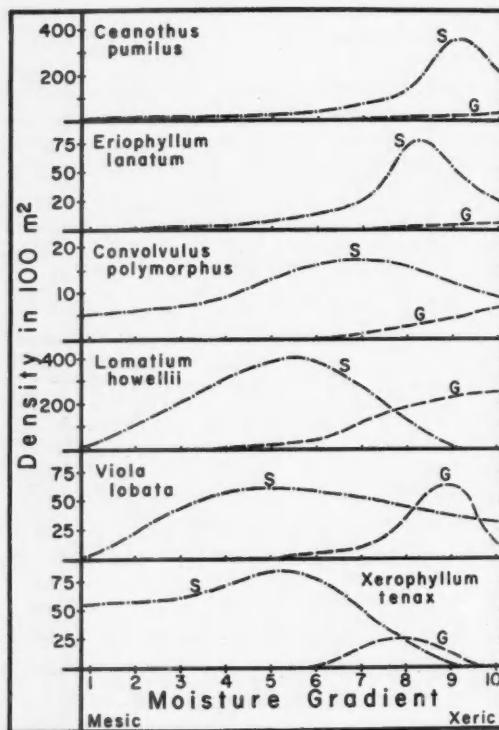


FIG. 24. Population distributions of undergrowth species on gabbro (G), and serpentine (S).

steps from gabbro to serpentine. Among 8 species compared from diorite to serpentine, several showed the 7.0 to 7.5-step displacement suggested by these values; the average was 6.5.

A second generalization suggested by the data is the individuality in species responses to the sequence of soils. Different species show all possible patterns of distributional response or "preferences" among the parent materials. The only relations to the parent materials which were not observed were the ideal ones which an ecologist might like to expect—sets of ecologically equivalent varieties or congeners replacing one another at comparable population levels on the three soils, or sets of clearly "associated" species with closely similar distributional relations to the three soils. The principle of species individuality (Rosenzky 1924, Gleason 1926, 1939), which is familiar in application to geographic areas of species and distributional relations to moisture and elevation gradients, also appears clearly in relations to parent materials in the Siskiyous.

A third conclusion suggested is the general occurrence of differences in stature or morphology when species populations occur on more than one of the soils—especially serpentine and non-serpentine soils. The phenomenon of "serpentinomorphism," the occurrence of morphologically distinctive forms on serpentine in species which also occur on non-serpen-

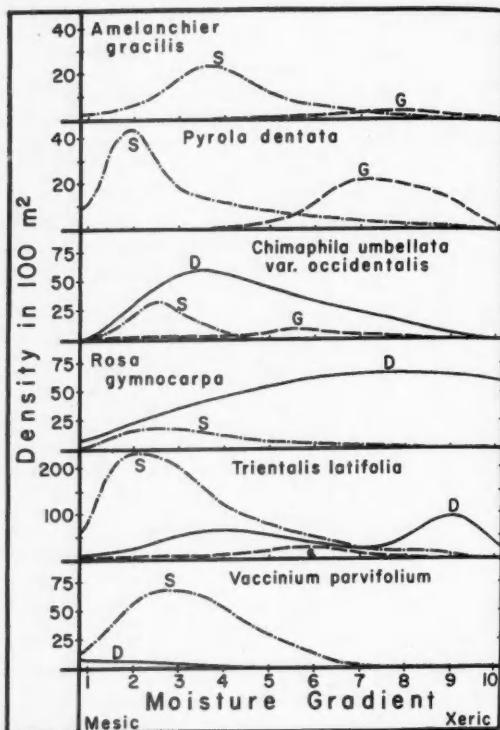


FIG. 25. Population distributions of undergrowth species on diorite (D), gabbro, (G), and serpentine (S).

tine soils, has been described in the European literature (Vilhelm 1925, Pichi-Sermolli 1936, 1948, Rune 1953, Ritter-Studnička 1956). It has been observed that most woody species occurring both off and on serpentine are of reduced stature on serpentine, or are represented there by smaller varieties. Even casual observation of herb species occurring on serpentine and non-serpentine soils permits recognition of serpentinomorph differences in leaf size, texture, and color, in pubescence, in stature and branching pattern—differences which in most cases suggest those which would be expected in a drier or more open environment. The environments on serpentine are in fact more open; a species whose population shifts toward the mesic 7 transect steps from diorite to serpentine is still in a community of less tree coverage and greater exposure to sunlight and evaporation on the latter. Genetic differentiation of serpentine ecosystems is known to be frequent among species occurring both on and off serpentine (Kruckeberg 1951, 1954).

RARE SPECIES AND SERPENTINE INDICATORS

Restriction to special soil materials is relative; Siskiyou species may be arranged in a continuous sequence from those observed on only one soil to those with substantial populations on all three. Expansion of the field of observation further illustrates the rela-

tiveness of parent-material restriction. Among species which might be thought "serpentine species" from their occurrence in the low-elevation transects, a whole series appear on diorite at higher elevations (*Pinus monticola*, *Arctostaphylos nevadensis*, *Quercus garryana* var. *breweri*, *Eriophyllum lanatum*, *Silene campanulata* var. *orbiculata*, *Eriophyllum lanatum*, *Erysimum capitatum*, *Monardella odoratissima* var. *glaucia*, *Epilobium paniculatum*, *Habenaria sparsiflora*, *Gilia capitata*, *Phlox diffusa*, *Eriogonum umbellatum*, *Holodiscus dumosus*, *Castilleja miniata*, *Angelica arguta*, *Lomatium macrocarpum*). Most of these occur on diorite in high-elevation meadows or on rocky summits, in communities as open and well-lighted as serpentine vegetation, rather than in forests. Conversely, a few low-elevation "diorite species" appear in the denser serpentine stands of higher elevations (*Arenaria macrophylla*, *Hieracium albiflorum*, *Iris chrysophylla*). Others of the "serpentine species" could be observed on soil materials (quartzite and argillite) that had little to do with serpentine and gabbro, but which supported vegetation somewhat more open and xerophytic-looking than that of diorite (*Silene campanulata* var. *orbiculata*, *Crepis pleurocarpa*, *Eriophyllum lanatum*, *Convolvulus polymorphus*, *Erysimum capitatum*, *Monardella odoratissima* var. *glaucia*, *Lotus crassifolius*, *Calochortus tolmei*, *Gilia capitata*, *Eriogonum umbellatum*, *Polygonatum muninum* var. *imbricans*, *Galium ambiguum*, *Lomatium macrocarpum*). Still other species largely restricted to serpentine within the study area occurred on non-serpentine soils in other parts of the Siskiyous (*Vancouveria chrysanthia*, *Balsamorhiza deltoidea*, *Eriophyllum lanatum*, *Hieracium cynoglossoides* var. *nudicaule*, *Arctostaphylos viscida*, *Rhododendron occidentale*, *Calochortus tolmei*, *Epilobium paniculatum*, *Phlox speciosa*, *Ceanothus cuneatus*, *Rhamnus californica* var. *occidentalis*, *Galium ambiguum*, *Lomatium triternatum*, *Perideridia oregana*, *Polygala californica*). For such species relative serpentine restriction, like relative community-type fidelity, is clearly dependent on extent of the field of observation of the species' distribution.

When these are eliminated from the list of "serpentine species" there remain a good number which both were rarely or never observed off serpentine, or serpentine and gabbro, and are fairly abundant and widely distributed in the main serpentine area (*Horckelia sericata*, *Balsamorhiza platylepis*, *Iris bracteata*, *Lomatium howellii*, *Epilobium rigidum*, *Calochortus howellii*, *Antennaria suffrutescens*, *Cordylanthus viscidus*, *Erigeron foliosus* var. *confinis*, *Aster brickelliioides*, *Schoenolirion album*, *Tauschia glauca*, *Sanicula peckiana*). Almost all these are endemic to the Siskiyou or Klamath Mountains. These and other species largely restricted to, but less widely distributed on, serpentine are truly rare species in the sense of restricted occurrence.

It has been suggested by Griggs (1940, cf. Rune 1954a) that rare species tend to occur in unstable, successional communities rather than climaxes. The

serpentine communities of the Siskiyous are climaxes in the sense of stability or self-maintenance (Whittaker 1954b), and are very old. Serpentine communities have existed in the Klamath Region through the Cenozoic, and the rich floras of these communities represent the product of millions of years of species evolution into and in climax communities on serpentine. Rare species occur in most varied circumstances; they occur where, according to the population characteristics of and environmental limitations for particular species, they occur. So far as concentrations of considerable numbers of rare species are concerned, however, the Siskiyou material is in accord with the hypothesis of Detling (1948a, 1948b) that concentrations of narrow endemics are correlated with concentrations of environmental extremes, and the emphasis by Mason (1946a, 1946b) of edaphic factors. In relation to succession and climax, it is suggested that such concentrations may be associated not with unstable successional communities, but with relatively stable or climax communities of environments which are distinctive or "extreme" and spatially restricted.

The group of species largely restricted to serpentine, but widely distributed on it, form a nucleus of "characteristic" serpentine species which might serve as indicators of serpentine soil. In practice, observing serpentine outcrops scattered through the Siskiyou Mountains, they were found to have little indicator value. Stands containing several of them were usually within the major serpentine areas and obviously serpentine vegetation; stands of smaller and sometimes unmapped outcrops, for which serpentine indicators were most needed, might contain one or two of these species, but usually none. The most useful indicators were found to be some of the stratal dominants of serpentine (*Pinus jeffreyi*, *P. attenuata*, *P. monticola*, *Quercus chrysolepis* var. *vaccinifolia*, *Xerophyllum tenax*, *Ceanothus cuneatus*, *Arctostaphylos nevadensis*) and other species of more frequent occurrence in smaller serpentine areas (*Galium ambiguum*, *Pyrola dentata*, *Lomatium macrocarpum*, *Cheilanthes siliquosa*, and in wetter sites *Rhododendron occidentale* and *Darlingtonia californica*). *Xerophyllum tenax* seems the most useful single indicator for small serpentine outcrops. Most of these are species of extensive occurrence on non-serpentine soils. In other areas they are wholly meaningless as serpentine indicators but within the Siskiyous their presence may suggest, though not indicate, serpentine soil.

VIII. CONCLUSION

One object of the present study was the analysis and description of a pattern of vegetation of much intrinsic interest; another was the further development of techniques for quantitative analysis of vegetation patterns. In the study as it has been developed in the preceding sections, various aspects of community relations have been brought into a system of quantitative treatment. In some cases the quantita-

tive analysis may seem only to provide numerical expressions for relations which an observant ecologist would detect without them, and yet may be well worth while for the additional clarity with which these relations are expressed. In other cases relations are revealed which are impossible to determine by field observation. Quantitative techniques can, when ineptly or mechanically used, obscure important ecological relations (Braun 1956). They can never substitute for effective observation, judgment, intuition, and scope of understanding; for only these can suggest which quantitative analyses are worth undertaking and provide evaluation and interpretation of the relations which emerge. Yet, in those studies for which the time-consuming sampling and analysis are feasible, techniques of gradient analysis may be productive for problems of both species autecology and community relations.

A central concept of the treatment in this work is the community-gradient or "coenocline" in relation to the topographic moisture gradient; these community-gradients are the units of comparison from one climate or parent material to another. It is felt that for some uses this approach has significant advantages over those centered on climatic climaxes or community classification. Any "system" for the study of natural communities is an integration of selected aspects of species and community relations, which can be investigated through a given, coherent set of concepts, to the neglect of other relations which cannot, and is necessarily more appropriate and productive in some circumstances than others. The limitations inherent in any approach or system may suggest the desirability of applying more than one approach to a given study when this is feasible—of supplementing a study in gradient analysis with consideration of classification as in the present work, a study based on classification with consideration of gradient relations.

Differentiation in relation to topography, and patterning in relation to patterns of topographic and other environmental gradients, are general characteristics of vegetation; and the concept of such patterning should be part of the ecologist's approach to interpretation of a present vegetation or a fossil flora. The terms *ecocline* and *coenocline* are suggested, not to name the obvious, but because of the need for these gradient-conceptions in the interpretation of relations of natural communities to environment. The vegetation of the Siskiyous can be conceived in terms of climax regions and vegetation units. One may regard the Mixed Evergreen Forests as forming a vegetational matrix for lower elevations in the central Siskiyous, a prevailing climax type in which the serpentine and other localized communities are dispersed, and which is replaced toward higher elevations by Montane Forest and Subalpine Forest climaxes, toward the west by Coast Forest, and toward the east by Oak Woodland, climaxes. But it is profitable also to conceive of the vegetation in terms of coenoclines changing in composition, physiognomy, and floristic relations in relation to climates and parent materials,

as a multi-dimensional pattern of vegetational gradients in relation to these environmental gradients. Thus the distributional relations of species, floristic groups, and community-types, and the interrelations of communities may be conceived through an abstract, conceptual "pattern" which is not simple, but brings into comprehensible form much of the still greater complexity of the vegetation itself.

The fact that the Southern Appalachians and Klamath Mountains bear comparable "central" relations to eastern and western forests has been commented on. One other parallel between these two mountain areas may be observed—their combination of unusual geological and biological interest with relatively undisturbed conditions. The Klamath Mountains are now, as the Southern Appalachians were some decades ago, relatively remote and little known. Partly because they are remote, extensive areas remain which are wild and natural. Both areas have exceptional scenic attraction; in the Klamath Region the coast of southern Oregon and northern California, the Rogue and other canyons, and some of the mountain landscapes themselves deserve to be more widely known—and, to the extent that is feasible, protected. Because the Klamath Region is not well known, it may be appropriate to observe that this is an area of biological interest as great as that of the Southern Appalachians: a comparable center of survival of ancient, Arcto-Tertiary forms in the Coastal Redwood and Mixed Evergreen Forests, an even greater concentration of rare species and remarkable floras, together with an unusually diverse range of floras and communities within a limited distance from the Coast inland, and as dramatic an expression of relations of natural communities to geological formations as is to be found anywhere in the world. There are many areas of biological and scenic value in the West, but among these the over-all interest of the Klamath Region is high, and suggests continued thought on long-range policies of utilization and preservation.

SUMMARY

I. Introduction

The Klamath Mountain Region, lying between the southern Cascade Mountains and Pacific Coast in northern California and southern Oregon, is an area of great climatic, geological, and vegetational diversity. One major range of the Region, the Siskiyou Mountains along the California-Oregon border, was chosen for a study of relations of mountain forests to climates and parent materials.

For reasons of vegetational history, the age of the Klamath Mountains, and the diversity of habitats in them, the Klamath Region is a "center" for forest floras and forest vegetation of the West.

II. Procedure

An area of quartz diorite in the central Siskiyou Mountains was chosen for intensive study of elevation

and moisture-gradient relations of vegetation on a more typical parent material. Low-elevation vegetation of olivine gabbro and serpentine was compared with that of diorite to study effects of parent materials. The change of vegetation from the humid coastal forests inland at low elevations, and serpentine vegetation at all elevations, were studied less intensively.

Gradient analysis techniques were applied to relations of species and communities to major environmental gradients. Within each 1000-foot elevation belt, or parent material, 60 vegetation samples representing all parts of the topographic moisture gradient were taken. Three techniques for arrangement of these samples into composite transects—by topographic classes of sites, by weighted averages of community composition, and by comparison with standards representing mesic, intermediate, and xeric sites—were used and evaluated. The weighted-average technique gave best results in this study.

III. Vegetation Description

Low-elevation diorite vegetation gradates from *Chamaecyparis lawsoniana*-*Pseudotsuga menziesii* forests in mesic sites, through *Pseudotsuga* forests with sclerophyll trees in intermediate sites, to sclerophyll forest with scattered *Pseudotsuga* in xeric sites. Low-elevation gabbro vegetation gradates from more open *Chamaecyparis*-*Pseudotsuga* stands, through more open sclerophyll-*Pseudotsuga* stands, to open, xeric *Pinus*-*Pseudotsuga*-*Quercus*-*Arctostaphylos* stands. Low-elevation serpentine vegetation gradates from still more open *Chamaecyparis*-*Pinus monticola*-*Pseudotsuga* mesic stands, through very distinctive forest-shrub stands with several conifers and two-phase undergrowth of sclerophyll shrubs and grass, to *Pinus jeffreyi* woodlands.

Toward higher elevations on diorite, the forests of *Pseudotsuga* and sclerophylls gradate into montane forests dominated by *Pseudotsuga* and *Abies concolor* at about 1200 m, and these into subalpine forests dominated by *Abies nobilis* and *Tsuga mertensiana* above 1800 m. Mosaic charts (Figs. 11 and 12) show relations of vegetation to elevation and topography on both diorite and serpentine.

IV. Climax Interpretation

All low- and most high-elevation vegetation of the Siskiyou Mountains has been affected by fires. Evidence from stand-curve analysis suggests, however, that the effect of frequent, less severe fires during the past century has been to reduce stand density without changing essential character of most stands. Different patterns of climax vegetation develop on diorite, gabbro, serpentine, and other parent materials in the Siskiyou Mountains. Any significant difference in parent material may imply difference in climax vegetation.

For a gradient of environmental complexes the term *complex-gradient* has been suggested; for the corresponding community-gradient the term *coeno-*

cline is here suggested; for the gradient of ecosystems comprising both of these the term *ecocline* may be used. The principal basis of the study was the comparison of moisture-gradient patterns, or coenoclines, from different climates and parent materials. Along a gradient from humid, maritime climates near the Coast to drier and more continental ones inland, the character of low-elevation coenoclines changes from *Sequoia sempervirens* and coastal *Pseudotsuga* forests, through mixed evergreen forests in the central part of the range, to a pattern of *Pseudotsuga* forest, oak woodland, and valley grassland in the Interior.

V. Problems of Classification

Formations, dominance-types, sociations, associations, and unions in the Siskiyou vegetation are discussed. The Mixed Evergreen Forests of conifers and sclerophylls are a prevailing climax of the Klamath Region and north California Coast Ranges. These forests are regarded as a major community-type of the West, and interpreted as a formation connecting the coniferous Coast and Montane Forests with the California broad-sclerophyll vegetation.

VI. Floristic Comparisons

Arcto-Tertiary forest remnants from opposite sides of North America, the Mixed Mesophytic and Mixed Evergreen Forests, have very similar life-form spectra, approximating: P 34, C 8, H 33, G 23, and T 2 per cent. The transformations of such "mid-temperate mesophytic" spectra along gradients of parent material, elevation, topographic moisture, and east-west climatic change in the Siskiyous are tabulated and discussed. The principal effect of the maritime-continental climatic gradient is in decreasing representation of evergreen forms.

Species diversities of plant communities increase markedly from maritime into continental climates, increase from diorite to serpentine, decrease along the topographic moisture gradient on diorite, and increase, then decrease, toward higher elevations on diorite. Such relations are not simply interpreted on the basis of environmental "favorableness." In the Siskiyous, community diversities tend to be higher in the more open communities, with more highly developed herb strata, of drier sites and climates and special parent materials.

Three aspects of species-diversity may be distinguished: richness in species of individual stands, degree of floristic change of communities along environmental gradients, and species-diversity of a community pattern or broadly defined community-type which results from both of these. Measurements of "coenocline differentiation" along the topographic moisture gradient, as one approach to the second of these, are discussed and applied. Coenocline differentiation increases from maritime to continental climates in the Siskiyous.

Measurements (coefficients of community and percentage similarities) show that the vegetation of

gabbro is floristically intermediate to that of diorite and serpentine, though physiognomically closer to the former.

Geographic relations of floras were studied through two approaches—representation of areal types, and average extents of distribution in different directions. Marked correlations of these geographic relations with local environments within the Siskiyous appear. The serpentine flora has a much higher representation of endemics, smaller average extent in all directions, but stronger southern or Californian affinity than the diorite vegetation.

VII. Relations of Species Populations to the Three Soils

Some Siskiyou species show evidence of population bimodality in relation to the topographic moisture gradient or elevation. Most species show a "shift toward the mesic," or displacement of their distributions toward less xeric sites, from diorite to gabbro and gabbro to serpentine. Rare species in this area are concentrated in stable or climax communities on special parent materials, especially serpentine.

VIII. Conclusion

Quantitative techniques of gradient analysis permit this complex vegetation to be analyzed and understood as a multi-dimensional pattern in relation to topographic moisture gradients, climates, and parent materials. The biological interest and scenic appeal of the Klamath Region equals that of the eastern center of vegetational and floristic diversity, the Southern Appalachians, and suggests further consideration of preservation of parts of the region for the future.

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